THE POPULATION DYNAMICS OF IMPALA (AEPYCEROS MELAMPUS LICHTENSTEIN) IN MKUZI GAME RESERVE

by

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Pietermaritzburg, 1979.

Unless specifically stated to the contrary in the text, everything contained in this thesis is my own original work.

for

Marilyn

Russell

Graeme

Trixie

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CHAPTER 1.

INTRODUCTION.

1.1. Purposes of this study.

The need for the rationalised management of a population of impala (Aepyceros melampus) became evident in the early 1960's, when conditions in Mkuzi Game Reserve changed dramatically, and the numbers of this species increased beyond what was considered to be the optimum carrying capacity of the reserve. The first major culling operations were based quite simply on this premise, without any scientific evidence for overutilisation of the primary resource.

After some early attempts at estimating the numbers of impala, it was decided in the late 1960's to conduct an intensive study of the population, its effects on the habitat, and its local seasonal movements. Because the population had become virtually an isolated one as a result of surrounding settlement and agriculture, it was seen as a unit with little interchange between the game reserve and neighbouring areas, except only for some southward movement onto adjoining State land.

The initial purpose of the study was to provide a basis for immediate management, and it was designed to include a number of factors which could be incorporated in long term planning.

1.2. The study area.

Mkuzi Game Reserve is situated in Zululand, north-eastern Natal, at the southern end of the Mocambique plain. It was established as a game reserve in 1912, having for some years prior

to that been an unofficial reserve under the care of the local magistrate. It is about 25 000 ha in extent.

The northern and eastern boundaries are formed by the Mkuzè river, which is a comparatively large, though seasonal, river. Surface flow ceases in most years for at least part of the dry winter season. The western boundary is surveyed and fenced, and follows approximately the line of the eastern edge of the Lebombo mountain range but has no ecological basis; it includes the foothills and, in some places, major features of this range, in the reserve. The southern boundary is merely a seasonal drainage line, which runs into a large shallow pan, Nsumu, which is also seasonal. This in turn drains into the Mkuze river in the south-eastern corner of the reserve which is largely a flood plain area, with drainages ill-defined. (See Figure 1.).

On three sides - west, north, and east - the game reserve adjoins densely settled land in which the main land use is pastoralism and agriculture, both shifting and established. To the south is unallocated State land, known as Nxwala, bounded on its south by the seasonal Msunduze river, and about 8 000 ha in extent. This land in turn adjoins State-owned farms on which cattle ranching and some agriculture are practised. At the time of the study, Nxwala was used as a grazing concession, with a maximum of 200 cattle permitted there at any one time. The fence between the game reserve and Nxwala was, and still is, no barrier to impala movement.

Topographically, Mkuzi Game Reserve may be divided into two main units: the comparatively flat terrain of the central and eastern sections, including the narrow riverine flood plain; and the western foothills region (See Figure 2).

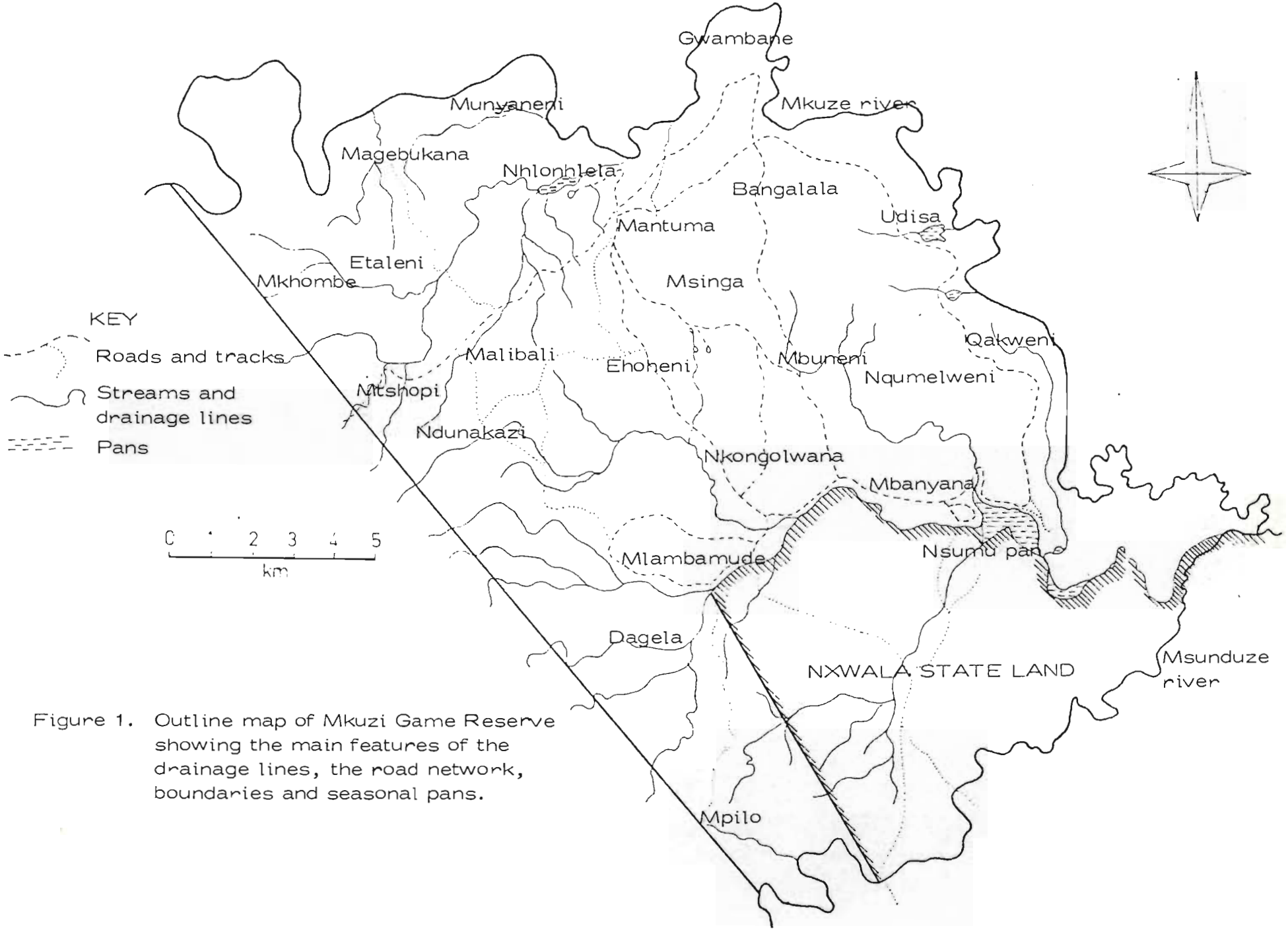

Figure 1. Outline map of Mkuzi Game Reserve showing the main features of the drainage lines, the road network, boundaries and seasonal pans.

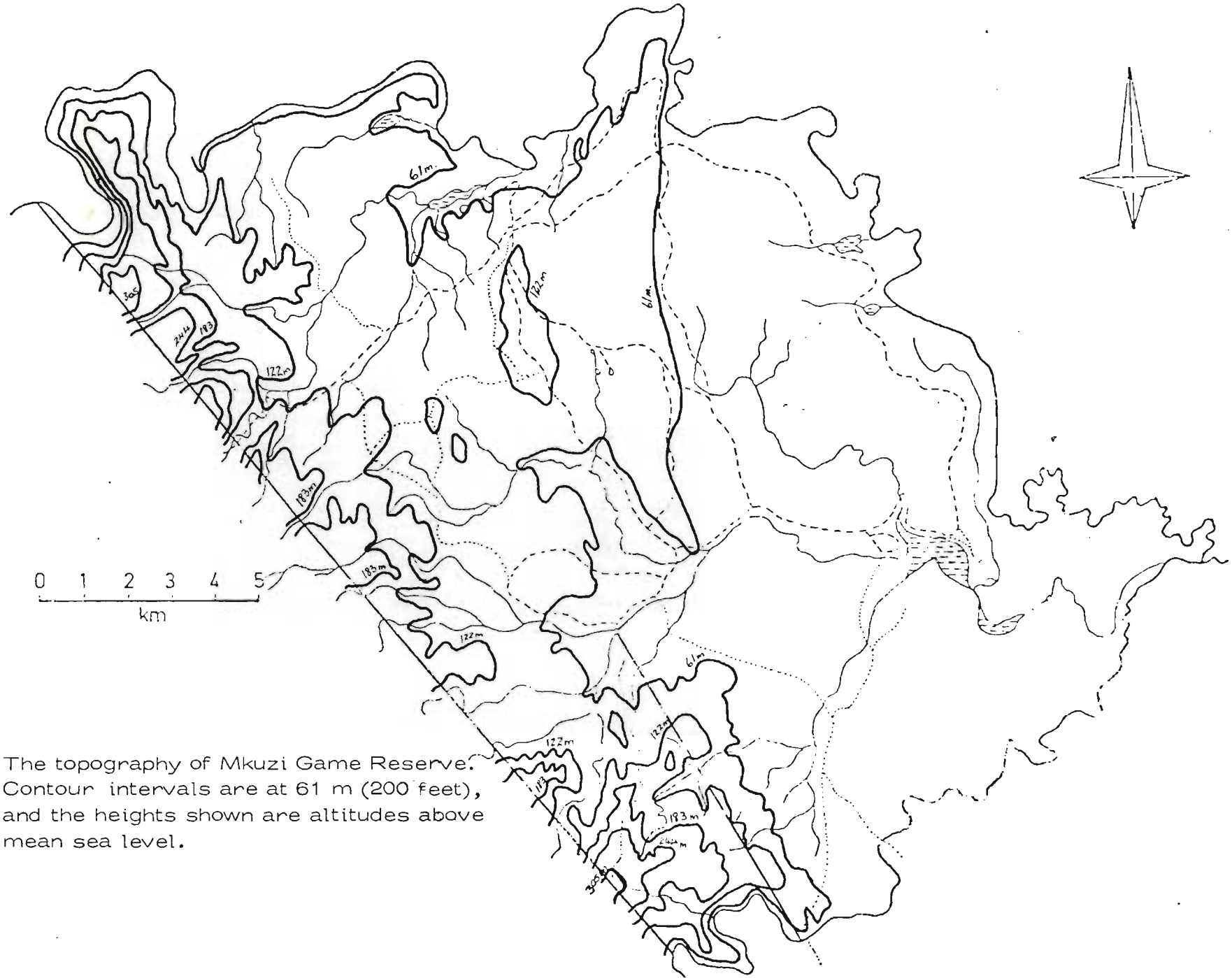

Figure 2. The topography of Mkuzi Game Reserve. Contour intervals are at 61 m (200 feet), and the heights shown are altitudes above mean sea level.

1.3. The study population.

The Mkuzi impala population has had a somewhat checkered history. There are very few references to the area what is now the game reserve in the writings of early hunters. In fact it can only be surmised in some books, e.g. Baldwin (1894), that the area was even traversed by pioneers, and little if any mention is made of the game species present.

Whilst game in many parts of Natal was seriously depleted in the latter part of the last century, other parts were left comparatively free from such destruction on account of the presence of tsetse fly, which was responsible for the transmission of nagana, or trypanosomiasis, a disease fatal to domestic cattle. With the settling of large tracts of land in Zululand in the early part of this century, pressure mounted for the eradication of game as a means of ridding the land of tsetse fly and of nagana. This pressure culminated in 1942 in the inception of a game eradication campaign in various parts of Zululand by the State Department of Veterinary Services. It centred on most of the game reserves in the area, and Mkuzi did not escape attention. Between March 1943 and February 1950 a total of 38 552 animals was shot in and around Mkuzi Game Reserve. Of these, 17 060 were impala (Unpublished records, Natal Parks Board files). During this period methods were developed of eliminating the tsetse fly by direct means, and shooting of game ceased as a result.

There is no record of the game populations in the 1950's, although about 400 impala were captured alive in the six years prior to 1960. Thereafter the need for more effective population control was recognised, and in the next five years 11 150 impala were removed by capture and shooting. The basis for this scale of

removal was largely by "rule of thumb", and it was only in 1964 that population control was placed on a more rational basis (Stewart and Stewart 1966). The numbers of impala that have been removed from Mkuzi Game Reserve are shown in Table 1.

The reserve supports comparatively few predators and the game reserve situation must be accepted as an artificial one on account of surrounding land use, which restricts the movement of the animals that occur there. The effect of these factors is a tendency for unregulated population increase, and consequent habitat overutilisation, to occur. Population control is therefore necessary, and although the first smallscale operations in the 1950's were primarily in the interests of public relations and of fulfilling the need to restock areas depleted of wildlife, the necessity for the removal of herbivores for the benefit of the habitat soon became a more important consideration.

Initially, and up to about 1960, a reasonable balance was maintained; surrounding areas were comparatively sparsely populated, and early reports (Natal Parks Board files) indicate that, although the river dried up less frequently than it does to-day, its depth during the dry season served as no barrier to impala movement. Therefore, emigration of impala from the reserve was relatively unrestricted. Furthermore, poaching was prevalent, and this factor, together with emigration, enabled the impala population to remain at a low enough level not to affect the habitat adversely.

To-day the question of overpopulation is an important one, and in order to maintain some stability in the habitat, the populations of herbivores are monitored annually, and their management is decided upon the basis of these results. The programme remains flexible, and can be changed at short notice when necessary. With external pressures on Mkuzi, in the form of settlement and agriculture,

Table 1. The numbers of impala removed during population control measures in Mkuzi Game Reserve since 1954.

Year	Shot	Captured	Total
1954		4	4
1955		10	10
1956		20	20
1957		103	103
1958		100	100
1959		151	151
1960	118	462	580
1961	237	666	903
1962	346	1 213	1 559
1963	1 567	1 352	2 919
1964	4 340	849	5 189
1965	3 045	671	3 716
1966	843	374	1 217
1967	624	592	1 216
1968	691	310	1 001
1969	559	788	1 347
1970	288	1 374	1 662
1971	449	2 148	2 537
1972	259	3 084	3 343
1973	126	2 168	2 294

increasing annually, the problem has become more acute. The last known large scale exodus of impala from Mkuzi took place in 1966 as a result of very severe water shortages in the reserve. (J.L. Tinley, pers. comm.). Many animals are known to have perished in this drought, both inside and outside the reserve.

Impala that move northwards or eastwards from the reserve are today harrassed and poached, and the only remaining direction for them to move is southwards, onto Nxwala State Land, south of which again movement is severely restricted by ranching and agriculture. The population of impala in Mkuzi Game Reserve and Nxwala State Land is therefore considered to be an isolated one, with very limited interchange with any other area.

In addition to the impala, which is by far the most numerous large mammal in Mkuzi, in terms of both absolute numbers and of biomass, other important ungulate species (not necessarily in order of importance or abundance) are wildebeest (Connochaetes taurinus), nyala (Tragelaphus angasi), kudu (T. strepsiceros), warthog (Phacochoerus aethiopicus), giraffe (Giraffa camelopardalis), black rhinoceros (Diceros bicornis), and zebra (Equus burchellii). There is also a small number of square-lipped rhinoceros (Cerathotherium simum). Several other species, notably elephant (Loxodonta africana) and buffalo (Syncerus caffer) are known to have occurred in the area but are now extinct there.

The only carnivorous mammals occurring in Mkuzi, which may have any significant predatory influence upon the ungulates, are black-backed jackal (Canis mesomelas) and cheetah (Acinonyx jubatus); the latter were reintroduced to the reserve in 1966. Spotted hyaena (Crocuta crocuta) and leopard (Panthera pardus) also occur in fairly small numbers, but no lion (Panthera leo) occur, the last one having been recorded as a vagrant in the early 1950's.

CHAPTER 2.

THE ENVIRONMENT.

2.1. Vegetation.

No comprehensive vegetation survey of Mkuzi Game Reserve has yet been undertaken. Moll (1968) recognised six basic vegetation types within the region, described by Acocks (1953) as Lowveld of the Tropical Bush and Savanna. These were as follows:

a. Tall tree savanna on the Lebombo mountains.
b. Short tree savanna on the flat plains adjacent to the mountains.
c. Tall tree savanna on the red loam soils.
d. Short tree savanna and thicket on the poorly drained, heavy black soils.
e. Tongaland sand forest.
f. Riverine woodland on the banks of the Mkuze river.

This classification unfortunately does not recognise the importance of other factors such as aspect, which may be significant in so far as impala habitat is concerned. Moll (1968) also pointed out that there is considerable overlap between the basic types, and that they are seldom distinct.

Bourquin (1973), using a species classification of the vegetation, distinguished seven basic types, adding only

grasslands to the six of Moll which are described above; the grasslands are limited to the mountain tops and to a small part of the flood plains. Again, the disadvantage of this classification is its failure to recognise impala habitat.

In this study, it was decided to use an essentially physiognomic classification, which served the main purpose of distinguishing favoured impala habitat. The nomenclature of Phillips (1969) was adopted.

2.1.1. Methods.

The most recent (1964) aerial photograph cover of the reserve was studied stereoscopically, and the boundaries of the obviously different vegetation types were marked on it and mapped separately. To confirm and augment the details, a ground survey was carried out over most areas of the reserve, covering the major vegetation types identified. In this survey, information on the physiognomy, the dominant tree species, and the composition of the ground cover were recorded. No quantitative data were obtained. A more detailed vegetation study is at present being conducted (P. Goodman, pers. comm.).

2.1.2. Results.

The vegetation was divided into the following broad sub-regions, with local variations described where relevant:

a. Lebombo mountains. This comprises a comparatively small area of the highest land along the western boundary, found mainly above the 183m (600') contour. The vegetation here

consists of sparse, open grassveld - sparse because of the high proportion of quartz in a very stony soil. Few trees are found, except in the pockets of deeper soil in the drainage lines; there the species composition of the trees resembles closely that of the lower-lying streambank vegetation.

b. Foothills. This sub-region extends along the length of the Lebombo mountains down to about the 122m (400') contour. The vegetation comprises two main facies. On the higher ground and steeper slopes is an almost pure community of Combretum apiculatum, the trees seldom exceeding about 6 m in height. Other species such as Ozoroa paniculosa and Dombeya rotundifolia are infrequent, the whole creating what Phillips (1969) describes as scattered natural, open woodland of medium height.

Along the lower slopes of the hills and ridges and forming a fringe to the Combretum woodland, is a community dominated by Acacia nigrescens. This too is essentially open woodland, although it is slightly more heavily wooded than the other facies, and consists of taller (6 - 8 m) trees of the dominant species. Again very few other species are present, and the community grades into streambank woodland (see (e)). Common shrubs include Grewia spp.

On the better developed soils of the lower-lying areas is a community of Sclerocarya caffra - Ziziphus mucronata open woodland, invaded in parts by Acacia karroo and A. nilotica, especially on what are thought to be old cultivated fields.

The Combretum woodland occurs on coarse soils derived

from the volcanic parent material of the Lebombo mountains, containing a high proportion of quartz; beneath the fairly shallow soil layer is basalt. Because of the porous nature of the soil it is well drained. The Acacia nigrescens woodland grows on poorly drained but deeper soils, which have a high clay content in keeping with their presence closer to the drainage lines. The Sclerocarya - Ziziphus woodland grows on the better drained soils.

Grasses in the Combretum-veld are primarily Aristida junciformis, with a small proportion of other, more palatable species, and a poor basal cover. Herbs are infrequent. Lower down the catena the grasses become rather more ephemeral, consisting of a high proportion of annual species. Herbs are more frequent, and the facies is a preferred habitat of impala.

c. Lowlands. This sub-region comprises the greater part of the reserve, and occurs below the 122 m (400') contour. Here there is a considerable variety of physiognomic types, and a corresponding variety in species composition. Because the topography is comparatively uniform, the most important single factor governing the distribution of the vegetation is the soil type. A wide range of soils exists in the lowlands - from pure white sand to heavy black clayey soils.

(1) Sandy soils. A characteristic feature of the reserve is the small patch of xeric sand forest. This is true forest, with dominant emergents such as Newtonia hildebrandtii, and upper canopy species such as Cleistanthus schlechteri, Pteleopsis myrtifolia, and Balanites maughamii. These large trees contain many epiphytes. The third layer of woody vegetation consists of

Gardenia neuberia, Commiphora neglecta, and Hymenocardia ulmoides; whilst a shrub layer with Salacia wardii and Croton gratissimus, and a poorly developed herb layer are also present. The sand forest is not a favoured impala habitat.

Flanking the true forest is a less-dense, medium height (8 - 11 m) woodland. This contains a greater variety of species than does the forest itself, and consists of several facies, depending on the aspect and the nature of the soil, which is mainly sandy. One such facies is characterised by Albizzia evansii, with Ziziphus mucronata, Schotia brachypetala, and Acacia burkei also present. The other important facies is a mixed woodland containing Acacia burkei, Terminalia sericea, Combretum molle, Strychnos spp., and Brachylaena discolor. In both these facies the grass cover is very sparse, but the species that do occur, such as Dactyloctenium australe, Eragrostis spp., and Digitaria spp., are palatable ones. This fact, together with the woody vegetation providing cover, make this community a favoured one with impala.

(ii) Loamy sand. Most of this soil type is red in colour, but it does grade into brown and grey in parts. Acacia species occur less frequently than on the clay, and the following are examples of associated dominant species in some of the facies:

Ziziphus mucronata - Acacia burkei.

Combretum molle - Sclerocarya caffra - Peltophorum africanum.

Spirostachys africana - Acacia nigrescens - Euclea spp.

Acacia nigrescens - Bolusanthus speciosus - Sclerocarya caffra.

Acacia nilotica - A. nigrescens.

These are all favoured impala habitat, largely on account of the fairly rich field layer of herbs and grasses.

(iii) Clay soils. These soils vary considerably in form, with a greater or lesser sand content, and cover more area of the reserve than any other type; the vegetation varies widely locally. It is essentially a series of variations on the theme "Acacia woodland", and forms a complex mosaic of which the commonest facies are:

A. grandicornuta - A. nilotica woodland.

A. nilotica - A. tortilis open woodland, often with encroaching Azima tetracantha.

A. luederitzii - Euclea divinorum thicket (with or without Spirostachys africana).

A. nigrescens - A. nilotica - Euclea spp. woodland.

A. gerrardii - Bolusanthus speciosus - Ozoroa paniculosa open woodland.

Many other species occur in these various woodlands, but it is quite impossible, without a quantitative analysis, to separate the communities more specifically. Impala favour these Acacia woodlands, but tend to avoid the thicket areas.

d. Riverine woodland. This is composed of a narrow fringe, varying in width from a few to several hundred metres, along the bank of the Mkuze river. The vegetation is a gallery forest, with Ficus sycamorus as an emergent, and Trichilia emetica, Acacia robusta, and A. xanthophloea also very evident. Characteristic of this forest are the scramblers, notably Acacia schweinfurthii and Combretum erythrophyllum, whilst thickets of Azima tetracantha form the understory in some areas. A well-developed field layer is found only in the open patches. Impala use this riverine belt primarily for cover.

e. Streambank vegetation. This is a woodland community, confined to the banks of seasonal streams. It contains Schotia

brachypetala, S. capitata, Acacia robusta, Sclerocarya caffra, Spirostachys africana, Olea africana, and others. In some places Acacia luederitzii forms a thicket fringe, and is probably an encroaching species. The streambank woodland provides cover for impala, and adjacent woodlands are heavily utilised.

f. Pans. Several large, seasonal pans are present in the reserve and are colonised by largely ephemeral communities of tall herbaceous plants and hygrophilous grasses, mainly Sporobolus robustus, Sorghum halepense, and Ischaemum africanum. Numerous smaller herbs are present, and under dry conditions this community is extensively utilised by impala.

Table 2 summarises briefly the relationships between the broad vegetation types described here, their physiognomy, and the soil types. Figure 3 is a vegetation map compiled from aerial photographs and ground surveys as described.

2.2. Soils.

Generally speaking the soils of Mkuzi Game Reserve are largely influenced by the underlying geological formations. On the steeper slopes of the Lebombo mountains the rhyolite has given rise to shallow, well-drained lithosols containing a high proportion of quartz. On the lower, less steep slopes are better developed soils, which have a gritty clay texture, are well drained, mainly grey, and are fairly shallow. In the bottomland situations, along the streams and drainage lines are alluvial soils which are fairly clayey and non-calcareous.

East of the area influenced by the Lebombo is the

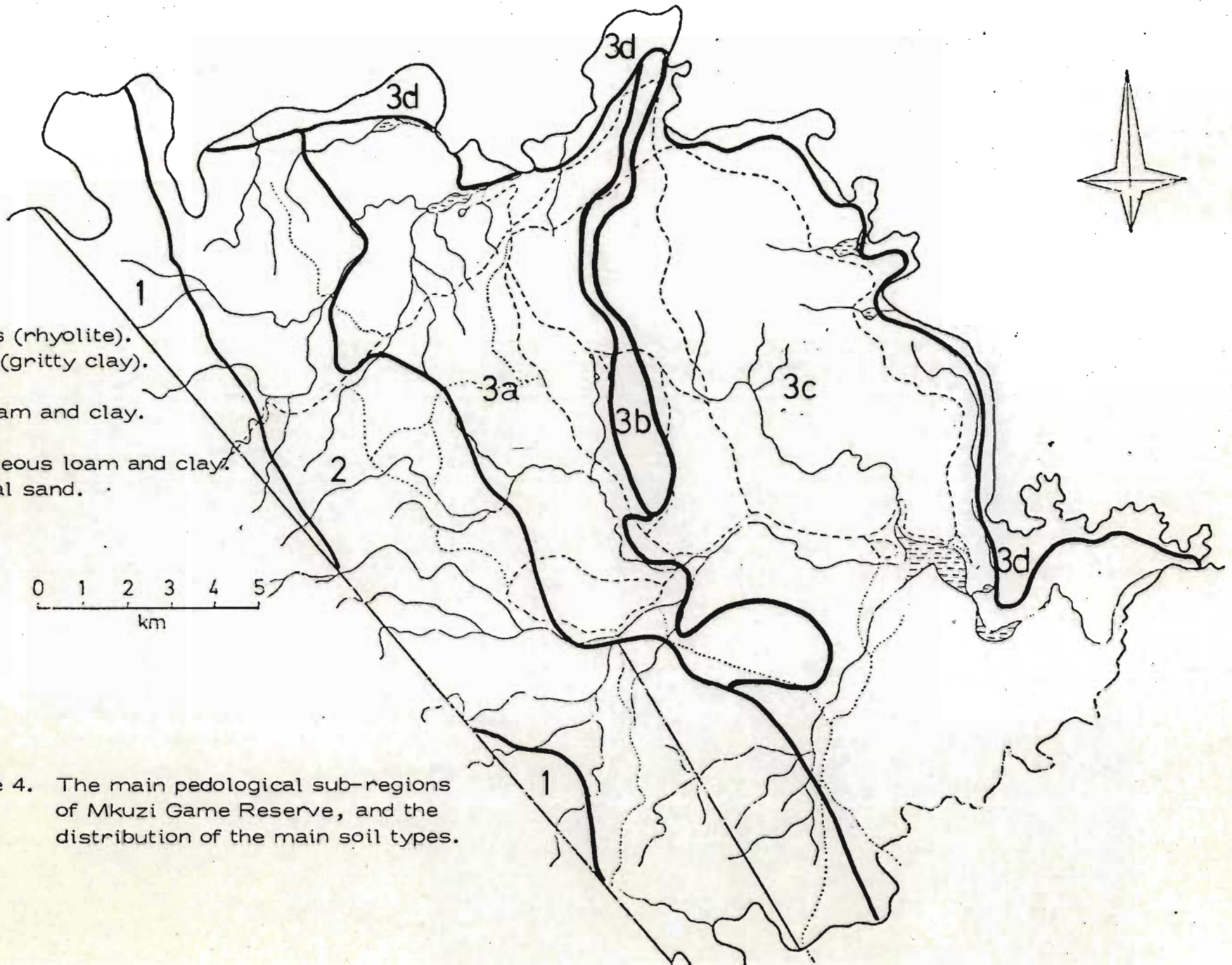

Figure 4. The main pedological sub-regions of Mkuzi Game Reserve, and the distribution of the main soil types.

year only in wet periods or after particularly high summer rainfall in the catchment. Otherwise it usually ceases to flow towards the end of the winter. In dry periods it may dry up earlier than this. Pools persist for long periods in the gorge, part of which lies in the extreme north-west of the reserve. The bed of the river below the gorge is sandy, while in the gorge itself there are rocky shelves which are fast becoming covered in sand.

The main tributary of the Mkuze river which flows through the reserve is the Nhlonhlela stream, in the north-west. This stream usually has flowing water during the summer months, but dries up during the winter season, leaving a few temporary pools, except in the wet periods when the pools persist. Before entering the Mkuze river it flows into a large seasonal pan which retains water throughout the year only during wet periods.

The Msunduze river forms only a couple of kilometres of the extreme south-western boundary of the reserve, and just touches the reserve again in the extreme south-east. However, it is very seasonal in nature.

In addition to the Nhlonhlela pan, there are several other seasonal pans along the Mkuze river, the most important of which is Nsumu. This large pan, whose southern edge forms the reserve boundary in the south-east, is fed by a number of seasonal water-courses, and its outlet is thought to be into the Msunduze river. However, because of the nature of the terrain at the Mkuze/Msunduze confluence, no clear watercourse is visible.

The main source of water for Nsumu is the Mkuze river which, when in flood, backs up the Msunduze river and overflows into the pan. It also regularly breaks its banks in the eastern part of the

reserve and flows down what is thought to be an old course, directly into Nsumu. This pan may hold water for several years at a time, but because of the prevailing dry period in the latter 1960's combined with the clearing of blockages in the lower Mkuze river, was dry for all of the study period, except for a single pool near the confluence, which contained water briefly.

All over the reserve are shallow depressions which contain either a clay-pan base or are underlain by impervious Cretaceous deposits. They retain water for varying periods after rain, but those in the west tend to dry out earlier than those in the east, where the Cretaceous deposits are closer to the surface and the soils are less pervious.

Because of the presence of stock on Nxwala State Land at the time of this study, water was provided for them in a trough at one point near the south-western corner of Nxwala. This was utilised by the impala in the area and may have influenced their movements out of Mkuzi Game Reserve during the late winter season.

2.4. Climate.

Because of its situation on the Mocambique plain, Mkuzi Game Reserve is essentially tropical, although comparatively dry. The summers are hot, and the winters mild; occasional cold spells accompanied by wet weather may be experienced in winter. Frost has been recorded only once - in June 1975 - when a light frost was recorded in the south.

Rainfall occurs mainly in summer, and falls either in the form of thunderstorms, or cyclonic rain accompanied by

southerly winds.

The prevailing winds are northerly to north-easterly, and these are generally warm and dry. The moisture-bearing winds, which are more frequent in summer than in winter, are southerly to south-westerly. Strong winds are not often encountered, except towards the end of winter, in August.

Mean monthly temperatures between 1963 and 1975, and mean monthly rainfall between 1955 and 1975, are shown in Table 3 and as a climatic diagram in Figure 5. From these data, a wet season from October to March and a dry season from April to September are evident. On average, 76,4% of the annual rain falls in the wet season and 23,6% in the dry. The mean annual rainfall for the 1955 to 1975 period is 597,2 mm.

Table 3. Mean monthly temperature and rainfall in Mkuzi Game Reserve.

Month.	Rainfall (mm) 1955 - 1975.	Temperature (°C) 1963 - 1975.
January	87,9	27,5
February	90,0	27,3
March	67,3	26,4
April	39,1	23,1
May	21,7	21,3
June	13,7	18,4
July	12,8	18,9
August	14,0	20,4
September	39,8	22,6
October	63,9	23,2
November	70,1	24,4
December	76,9	26,3
Total	597,2	

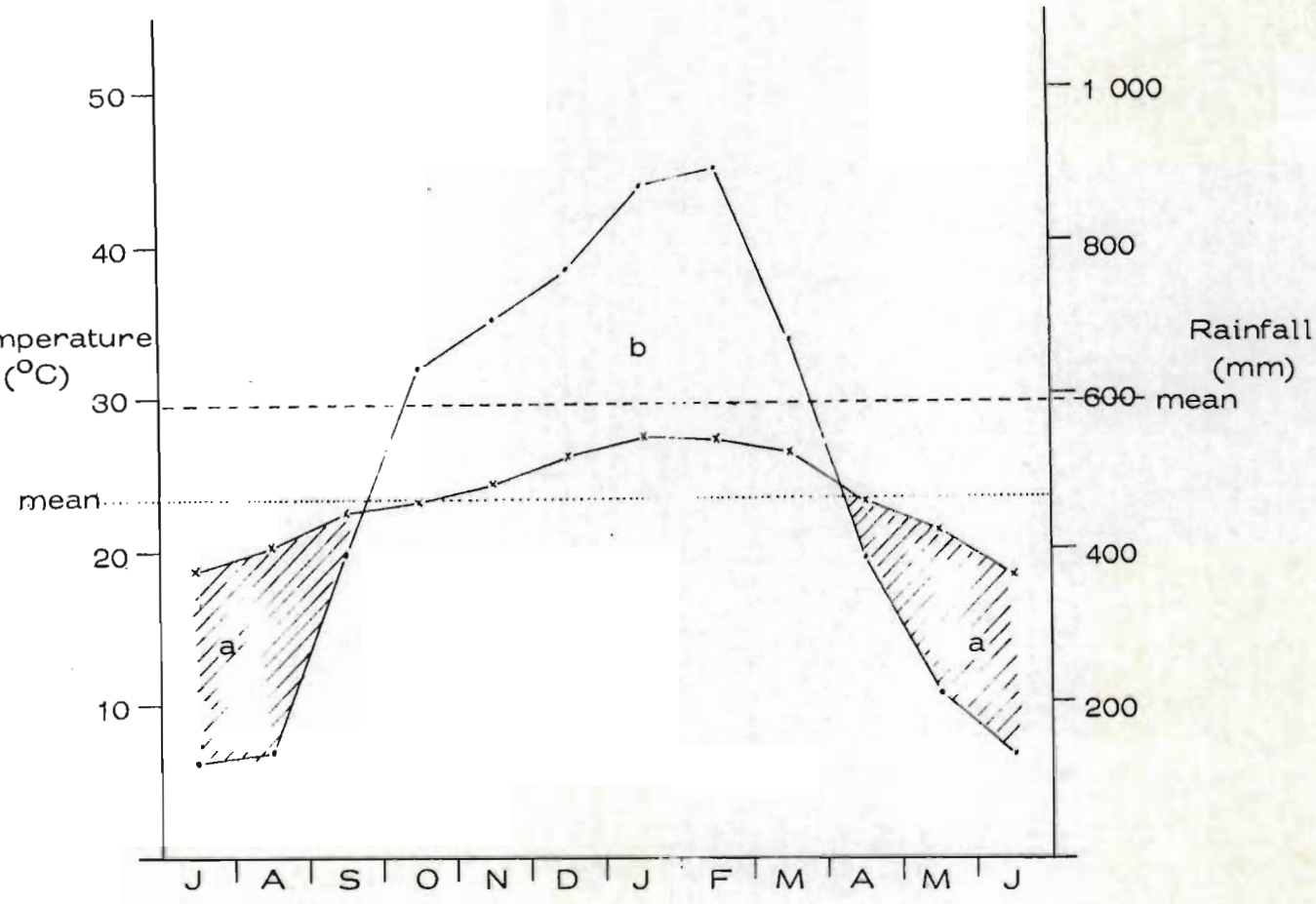

Figure 5. Climatic diagram for Mkuzi Game Reserve, Mantuma.
Rainfall - 21 year mean, temperature - 13 year mean.

•——• Monthly mean precipitation (mm).
×——× Monthly mean temperature (°C).
..... Mean annual temperature.
------ Mean annual rainfall.
a. Dry season.
b. Wet season.

CHAPTER 3.

HABITAT RELATIONSHIPS OF IMPALA

3.1. Introduction.

No matter how well adapted a species may be to particular conditions, there are certain basic requirements and resources upon which that species is dependent for survival. These may be identified as food, water and cover. Obviously the habits of a species will dictate its habitat requirements. In addition to these basic needs, there are also interactions of the species being studied, with other species and the environment, which must also be considered.

Survival of a species depends upon its reproduction, population growth and distribution, and all these characteristics are dependent upon its relationships with the environment. Each will be considered in later chapters, whilst in this chapter the basic requirements of impala, generally and specifically in Mkuzi, will be considered.

3.2. Cover.

Lamprey (1963) described the impala, in the context of his study area in Tanzania, as an "open woodland species", frequenting the boundaries between open/dense, open/moderate, and very bare/open cover. Such habits enable the animals to find cover easily, and at the same time to obtain all their food requirements.

Although not a comparable situation, Jarman (1972) showed that on the Zambezi flood plain, at times when it was not inundated, impala were fairly catholic in their selection of habitat, preferring open grassland when the grass was young, and moving into broad-leafed woodland when the grass became rank - this despite the presence of Acacia woodland in the same area.

During the present study, most of the impala were encountered in what Phillips (1969) described as "open woodland", "woodland", or the intermediate "woodland/open woodland transition". The first mentioned, by definition, requires that the crowns of the constituent trees be at least 20 metres apart; in woodland they touch or overlap. This bears out Lamprey's (1963) contention that the impala is essentially a frequenter of open woodland.

Much of Mkuzi Game Reserve consists of one of these three physiognomic types, the composition and structure varying considerably from one area to another. Impala showed a preference for both Acacia and broadleafed woodland, indicating that dietary and cover requirements were found in both types.

3.3. Diet.

The impala is a mixed feeder, that is it both browses and grazes. The proportions of woody plant material and grass that are consumed apparently vary at least seasonally, if not regionally as well. The variation is apparent from the observations that follow.

Talbot and Talbot (1962) recorded a diet for the impala consisting of 56% grass and 44% other food, namely browse in the form of woody plants and herbs. Lamprey (1963) found by direct observation, on the other hand, that 92,5% of impala seen were grazing, 6.3% were browsing on woody plants, and only 1,2% feeding on herbs. He attributed the difference to either the method of observation or differences in the availability of the respective diets. Most of the impala observe by Lamprey occurred in his transects during the wet season, when grasses were succulent and therefore preferred.

Jarman (1971), using a method of direct observation, noted a distinct preference for herbs and woody plants: out of a total of 817 feeding observations on impala, only 38 (4,7%) were of grasses, over a study period covering three years. Grass in Jarman's study area was very sparse, which tended to favour the presence of browsing species, and probably accounted for the predominantly browsing habit.

Avazedo and Agnew (1968), in analysing rumen samples from a population in the Kenya Rift Valley, reported on a very much higher proportion of grasses than browse material in the faeces - up to and more than 95% grass in a sample taken at the end of the dry season. Another quantitative study was that of McAllister (1967) who, in reporting on a population at Nagle Dam in Natal, found that the ratio of monocotyledonous to dicotyledonous material in the faeces was 1,67:1 - again indicating a preponderance of grass in the diet. Hitchins (1968) also recorded grass in the diet, but gave no indication as to its relative proportions compared to other plants.

It is therefore not possible to arrive at any conclusion,

from examination of the literature, on the food preferences of impala. In the present study, no quantitative data on this subject were obtained, although from direct observations, there is evidence that impala graze more frequently during the wet season, when the grass has a high moisture content. With the onset of the dry season, the grass becomes brittle and unpalatable, and impala rely more heavily on woody plants.

As a grazer, the impala is highly selective for young shoots, annual grasses, and stoloniferous grasses.

3.4. Water.

Impala are apparently not completely dependant upon surface water every day: for instance Lamprey (1963) reports having seen impala about 40 km from the nearest source. He concluded that they derived sufficient sustaining moisture from the dew-covered grass in the early mornings, whilst also making use of metabolic water derived from the food eaten, and utilising various physiological means of conserving body fluids. Young (1970) noted that impala in the Kruger National Park drink very infrequently. This is true of the summer season, but in the very dry winter they are more dependent on water, presumably because of the low moisture content of the food material. Despite this M.V. Jarman and Jarman (1973) suggest that impala may drink only every second or third day even in the dry season.

Water availability in Mkuzi creates a situation whereby for much of the dry time of the year, those species which are dependent on surface water are forced either to remain within reach of the two artificial waterholes in the centre of the reserve, or to move

southwards onto Nxwala State Land where permanent water is available - both there and to the south, on the farms. If Lamprey's (1963) conclusions are correct and applicable to impala in Mkuzi then impala movements there would not be affected. However, since water is present, they probably rely on it to augment other sources.

During the dry winter season in Mkuzi, the dew is generally very heavy, and impala were seen to be particularly active just before, and for some time after, daybreak. Furthermore, impala were seen up to 8 km from the nearest source of surface water even in the driest time of the year, suggesting that in Mkuzi too, they do not necessarily drink every day. However, since this is not an undue distance to move for water it is probable that they did do so from time to time, and did not rely solely on dew and metabolic water. Later analysis of impala distribution demonstrates the relationships with permanent surface water.

3.5. Habitat management.

Along with the management of certain species of large mammal is a planned programme of habitat management. This is necessary because of the artificial situation created by the nature of the reserve. It takes the form of control of erosion in the very erodible soils of the area; of exotic plant eradication, particularly along the floodplain where seeds of such species as syringa Melia azedarach and prickly pear Opuntia spp. are deposited by the river; and burning. A system of rotational burning of the foothills region has been instituted although the veld is subject to inspection every year before burning. The system is not a rigid one. Burning takes place after the first spring rains have fallen. Its effect is to remove the accumulation

of litter and to provide young, green grass for grazing species. This in turn relieves the pressure on adjacent areas at a critical time of the year, as grazing species are attracted to the burnt areas.

A further objective of burning is to try to reduce the quantity of Bothriochloa insculpta, un unpalatable grass which is utilised only briefly when young shoots are present, such as after a burn, and which occurs fairly extensively in the Acacia nigrescens open woodland adjacent to the foothills. Elsewhere in the reserve the grass cover is seldom sufficient to burn effectively and in any event the practice is not considered necessary.

In a few parts of the reserve, experimental thinning by mechanical means of encroaching woody plants has been attempted. This applies particularly to Azima tetracantha which has formed quite extensive thicket patches in the eastern part of the reserve, and to Dichrostachys cinerea which is tending to encroach in the Acacia nigrescens - A. nilotica woodlands in the mid-western parts.

During the anti-nagana campaign in the 1940's, attempts were made, as a means of reducing the cover available to tsetse flies, to control the thickets of Acacia luederitzii, but the plants regenerated fairly rapidly without the association significantly changing in character or composition.

3.6. Habitat utilisation by impala.

It is evident from Chapter 2.1.2 that there is a very close relationship between the soils and the vegetation in Mkuzi. The soils, and consequently the vegetation, demonstrate what can perhaps be described as a catenary sequence from the volcanically

derived soils of the Lebombo mountain foothills, through those derived from the cretaceous sediments which underly most of the lowlands and which are masked in places by Tertiary sands, to the Recent sediments comprising the floodplain and drainage lines.

The drainage and depth of these soils play an important role in determining the vegetation and consequent use of the various regions by impala. On the slopes of the Lebombo foothills, where the soils are shallow and well drained, the grass cover is generally sparse and the species have poor food value. Consequently these areas are not preferred impala habitat, except for a short time when the grass is young and tender and after burns when the grass is green. Browse plants are infrequent in this part of the reserve.

At the foot of the slopes, in the Acacia nigrescens and Sclerocarya - Ziziphus woodlands, the soils are less well drained, so that the grass species composition is quite different and edible herbs are more frequent. The climax grass in most of these areas is Themeda triandra, but this has, through past overutilisation, particularly by wildebeest, been largely replaced by the inedible Bothriochloa insculpta. The herbs still play an important part in the diet of impala for a great deal of the year, while some of the smaller woody plants are also utilised, particularly the encroaching Acacia shrubs. These areas are favoured impala habitat during the wet season, and less so in the dry season.

The bulk of the lowlands, with their sandy to clay soils and wide diversity of vegetation types, provide abundant food and cover for impala throughout the year. Early in the wet season there is a dense ground cover of herbs and grasses, which is utilised by impala

throughout the summer months, although the presence of food in the foothills region at this time does, to some extent, result in dispersion to these areas. During the hottest period of the year, in January and February, the impala in the foothills remain in the vicinity of the drainage lines where shade is available.

The early part of the dry season is important from the point of view of impala, for it marks the change from a predominantly grass/herb diet to one of browse. The deciduous trees start to drop their leaves from about June, and the fallen leaves of some species, particularly Ziziphus mucronata, form a fairly important part of the diet. Following this, the Acacia species, particularly A. nilotica and A. tortilis, drop their fruits, and these are highly favoured by several herbivores.

The most critical period for impala is the latter part of the dry season - August and September - when the only food available is the leaves of trees. Competition with other browsers such as nyala and kudu is at its keenest and, because both these species are able to reach higher than impala, the impala must resort to less preferred browse species or seek other, less preferred areas. Nyala are particularly sedentary in their habits, and are thus the most important competitors of impala. There is thus a tendency for impala to move out of Mkuzi at this time, and the only direction left for them to move is south. This feature is discussed in a later chapter.

As conditions become wetter in October and the day length increases, grass starts growing, and trees start sprouting new foliage. The competition between herbivores is no longer critical, and the impala, particularly females, are able to start storing reserves for the lambing season and lactation period.

The daily routine of impala differs between the wet and dry seasons. In summer there is usually abundant surface water over most of the reserve, so that daily movements are very restricted and herds comparatively sedentary. In exceptionally wet seasons, some of the streams and drainage lines in the foothills retain water throughout the dry season, mainly in pools, although the Nhlonhlela stream in the sorth-west of the reserve may continue to have flowing water. In the lowlands, some of the pans also retain water for quite long periods. At the end of the dry season, even after average and above average summer rainfall, most surface water is absent, except for the two artificial pans, and pressure on the vegetation in the central region becomes intense. Although they may not drink every day, many impala must move considerable distances to water at this time, particularly when their home ranges are near the edges of the reserve. Competition, both inter- and intraspecific, for food resources precludes residence in the central region, which becomes heavily utilised at this time. This was noted by Dixon (1964).

Both the study years 1970 and 1971 were comparatively dry, and followed several dry seasons of below average rainfall. Consequently movements due to environmental influences were well marked, and are probably not nearly as marked in periods of higher rainfall, such as has been experienced since 1972.

A particularly disastrous year occurred in 1966, when it was not possible to sink a well point deep enough into the sandy bed of the Mkuze river to reach water for pumping to the artificial waterholes. These therefore dried up, and impala were forced to move out of Mkuzi Game Reserve in large numbers. Many returned after the first rains, but others remained outside, and a fair number perished. The conditions

in 1966 emphasised the need for management, for it demonstrated what were probably the prevailing conditions prior to the establishment of the first of the permanent waterpoints some 20 years earlier. At that time impala, and presumably other species as well, probably left the reserve, reducing the pressure on the habitat that is prevalent and so evident today.

3.7. Modification of the habitat by impala.

Although it is no longer so marked, in the 1960's, when the population is thought to have been a good deal higher than it is now (Stewart & Stewart 1966), a very obvious feature of the Mkuzi landscape was the presence of a distinct browse line on certain species such as Acacia tortilis and A. nilotica, both preferred food plants of the impala. Associated with this was a ring of bare ground around each tree or bush clump where impala, in reaching for the browse and seeking fallen seed pods (a favourite food), had seriously trampled the grass layer. Even under present conditions this becomes so severe in most winter seasons that the nature of the grass layer has changed from perennial species to annual ones. These latter manage to establish themselves after rain, when the impala become more spread out because of more readily available fodder elsewhere. This change in turn, has the effect of inducing the impala to return and further to graze the affected areas for, not only is it apparent that impala prefer secondary growth, in this case in the form of annual grasses and herbs, but the presence of shade beneath the trees is an added attraction in itself.

In this way then, and also because of the tendency of impala to remain fairly sedentary on a small area of range, the species is able to modify the habitat to suit its own preferences. This

tendency to "sit" on certain areas is part of a cycle of heavy utilisation resulting in the establishment of more palatable and preferred annual grasses and herbs, resulting in turn in further heavy utilisation.

3.8. Other herbivores.

The presence of other herbivores in Mkuzi Game Reserve provides varying degrees of competition with impala at different times of the year. The most important of these are:

(i) Wildebeest. This is a purely grazing species, widespread in the reserve, but found mainly in the open savanna woodlands of the lower ridges in the western region, and in some of the more open Acacia woodlands of the lowlands. Its influence on the grassveld is quite considerable, and the population in 1970/71 stood at an estimated 1 200 animals. Competition with impala is not very great, for the wildebeest is a bulk roughage feeder (Mentis, pers. comm.), and feeds on coarser grasses than those selectively grazed by impala.

(ii) Zebra. Like the wildebeest, the zebra is a bulk roughage feeder, restricted to better grassed areas in the west, but occurring where suitable grass occurs in the lowlands as well. The numbers in 1970/71 did not exceed 120 animals.

(iii) Warthog. This is a common species over most of the lowland area. It is a highly selective grazer, preferring succulent grasses and tender shoots, mainly within 10 cm of the ground (Ewer, pers. comm.). As such it competes with the impala, but mainly at that time of the year when suitable grasses are abundant. It is very dependent on surface water. Its numbers are very difficult to

Table 4. The approximate numbers and biomass of herbivore species in Mkuzi in 1970/71.

Species	Approximate population	Approximate biomass (kg)
Impala	17 000	800 000
Wildebeest	1 200	250 000
Zebra	120	20 000
Warthog	2 000	80 000
Nyala	1 500	100 000
Kudu	500	60 000
Giraffe	30	12 000
Rhinoceros (white)	4	6 000
Rhinoceros (black)	35	28 000
Steenbok	500	7 500
Grey duiker	500	10 000

estimate at the best of times and, because of the succession of dry years preceding the study period, the population was at a low ebb, and probably did not exceed 2 000 individuals.

(iv) Nyala. The nyala is predominantly a browser, even in the wet summer season (Vincent et al 1968), although it does graze as well when the grass is new. The nyala is restricted mainly to the dense woodland and thicket, but does also enter more open woodland. It is larger than the impala, and is therefore able to reach a higher browse level. However, it is very dependent on surface water and does not move great distances, and for these reasons is restricted during the dry season to within a couple of kilometers of permanent water. The nyala is thus a very important competitor for food and for favourable habitat, with the impala.

The numbers of nyala are very difficult to estimate, but local residents were conscious of the fact that the population in 1970/71 was not nearly as high as it was prior to the drought of 1966, and probably did not exceed 1 500.

Less important species from the point of view of competition with impala are kudu, giraffe, steenbuck Raphicerus campestris, grey duiker Sylvicapra grimmia, and square-lipped rhinoceros, the first two because of different feeding levels, and the last three because of relative numbers and biomass.

In terms of biomass, the impala, during the study period, was by far the most important herbivore in Mkuzi. This can be seen from Table 4. Thus the total biomass of other herbivores is less than 75% of impala alone, and the main impact on the habitat is that of impala. Impala make up 58% of the total biomass of the reserve.

3.9. Carnivores.

Carnivores present in Mkuzi are insufficient to have a serious impact on the impala population. Cheetah, which were reintroduced in 1966, are the only ones which prey on adult impala, although very few kills by cheetah had been recorded by 1971. Only 20 were introduced, and it is not known how many of these survived. They are infrequently seen, and in two years of regular road strip sampling I only saw one myself.

Jackal are very common in Mkuzi, and have frequently been recorded at the carcasses of juvenile impala, but it has not been possible to say with any certainty whether these were killed by jackals or simply found dead by them. There are several records of jackal chasing juvenile impala, but very few observed kills.

There is a small population of hyaena, and no known instances of kills by them on impala, with the sole exception of one case in which a hyaena took an adult female out of a herd which was being followed at night for culling by spotlight. This was probably an exceptional case, for hyaenas had become accustomed to following the culling vehicles to collect entrails from animals which were gutted in the field.

3.10. Management of herbivores.

Because of the overwhelming impala biomass, this species has been the main target of management. However both wildebeest and warthog numbers have also been controlled. In the case of wildebeest this has been because of their observed impact on the habitat, and in the case of warthog it has been because their body condition frequently drops to serious levels because of lack of food.

Warthog were particularly hard hit by the 1966 drought, and the numbers seriously depleted. Consequently it was not necessary to carry out any large scale population control for a few years after that.

In 1963 and 1964 the numbers of impala in Mkuzi reached a very high level of nearly 20 000 (Stewart and Stewart 1963, 1966). Coincidental with this was a serious overutilisation of the habitat, attributed to the effect of the impala. It was therefore decided to reduce numbers by at least 5 000 (see Table 1), and thereafter to try to maintain a population of 12-15 000 until the effects could be assessed. These plans went awry after the 1966 drought, with the result that the estimated annual increase was lower than anticipated. The numbers built up rapidly again until 1971, but the population was not checked adequately, with the result that overutilisation was again evident by this time.

The objectives of management are to maintain species diversity in terms of both animals and plants. For this reason, it is considered important to avoid serious overutilisation of the resources and consequent possible deterioration, or even destruction, of any one vegetation type. Because of the complex mosaic of vegetation types in Mkuzi Game Reserve, it has not been possible to identify any one in particular which is threatened, so that impala population control has been directed simply towards an overall reduction rather than selective reduction in specific areas. Because of naturally higher densities in certain vegetation types, these areas have received more attention, but the tendency is always towards replenishment of these areas from other, less favourable ones, and from annual recruitment.

CHAPTER 4

POPULATION ESTIMATION

4.1. Historical background.

Prior to 1963 there is no record of the status of impala in Mkuzi Game Reserve. In that year a series of road strip counts was carried out (Stewart and Stewart 1963), in order to analyse the sex ratio prior to removing a number of individuals of one sex in an effort to change the sex ratio and so to determine the population size. The results of the second series of counts were reported by Stewart (1964), and the final population analysis by Stewart and Stewart (1966).

By this change-in-ratio method (Hanson 1963), the population of impala was estimated as nearly 20 000. The technique, as carried out in Mkuzi, has severe limitations, for the efficiency depends probably more than in any other technique upon the accuracy of the sampling.

Following this, Vincent (1966) carried out a road strip census based on the King method (described in Giles 1969). This resulted in a population estimate of about 16 000 impala which, incidentally, when the number of animals removed in the interim and the estimated recruitment were taken into account, compared very favourably with the earlier estimate of 20 000 (Stewart & Stewart 1966). No refinements such as stratification were attempted however, and, as will be shown later, the method does, theoretically anyway, have the effect of overestimating the population.

In 1969 the first attempt at aerial census was made. A

single-engined four-seater Cessna aircraft was used, having been tried successfully for counting square-lipped rhinoceros and other large species such as buffalo, wildebeest and zebra in another area. The method used was to fly a series of parallel strips at an altitude above the ground of about 200 m. An observer on either side of the aircraft counted animals seen on his side and called the results to a recorder seated next to the pilot. It was found to be very difficult indeed, to observe impala under the conditions of altitude and speed - about 80 knots - and less than 2 000 impala were counted, despite the fact that the entire reserve was scanned with the exception of the blind strip beneath the aircraft which is discussed in Chapter 4.2.3. A simple ground check shortly after the aerial count revealed more than 1 000 impala visible from the roads alone.

Graham and Bell (1969) quantified the counting rate of an observer using a fixed-wing aircraft. They assumed an average counting rate of three animals per second. At an air speed of about 80 knots, it takes about 2,5 seconds to travel 100 metres, so that in theory only 7,5 animals could be counted for every 100 m covered. In addition, it is necessary for the observer to cast his eyes over a predetermined strip width of up to 500 m so that the necessity to look for animals under trees, in different conditions of light and shade, makes the task even more difficult. For a herd species which is also fairly small and well camouflaged from the air, such as the impala, the technique is totally impracticable, even when numbers in herds are estimated, and no reliance can be or has been placed on the results.

4.2. Helicopter census.

In 1970 a helicopter was used for the first time to count all species in Mkuzi. Two separate counts were carried out in May and August of that year. This method was used in each subsequent year,

when the technique was the same, but different observers were used. The helicopters used were a Bell G-5 in 1970, a Bell G-4a in 1971, 1972, and 1973, a Hiller HU 12e in 1974, and a Hughes 300c in 1975, 1976, and 1978. These machines are all capable of carrying a pilot and two passengers, with some discomfort to the passenger in the middle - as I found to my cost.

4.2.1. Method.

The passenger door on the right hand side of the aircraft was removed for improved visibility. In the 1971, 1972, and 1973 counts this was more particularly to facilitate the individual identification of black rhino Diceros bicornis. All species were counted and recorded however.

The reserve was arbitrarily divided into blocks with convenient, easily recognizanle boundaries such as roads, tracks or drainage lines. These blocks in no case exceeded about 3 km in any one direction. The reason for this limitation in size was to avoid the possibility of the aircraft drifting off a predetermined course because of the length of each run. A further advantage of the small counting blocks, and hence of short flight paths, was that the observers were better able to remember and recognise a particular herd, or even individuals, on the return path, thus obviating a lot of double counting.

Once the direction of the initial flight path in each block had been established, the same compass bearing and its reciprocal were used alternately for sugsequent flight paths in the same block. Generally speaking however, it was possible for the pilot to navigate on physical features, except in certain parts of the reserve where the compass was essential due to the lack

of features and the low altitude at which flying took place. The effect of this operation was a series of parallel flight paths across each counting block, the distance between them varying, according to the nature of the vegetation, from 50 m to about 200 m. The counting height was, on the average, about 30-50 m above ground level - or higher in open country - and the best speed for ease of observations was found to be about 60-80 km/h.

Since, in the helicopters used, the pilot was seated on the left side of the craft, the two observers were seated in the middle and against the right hand side respectively. The latter scrutinised a strip to the right of the flight path, whilst the former, with more visual interference and discomfort, scanned the strip immediately beneath the aircraft and slightly to the left of the path. On the reverse traverse, the observer on the inside of the turn was then, if necessary, able to create an overlap with the strip just examined by him, simply by casting his eyes farther out from the line of flight. Alternate left and right turns at the end of successive runs were made of course, so that the need or lack thereof, to create this overlap fell to the lot of each observer in turn.

Sightings of animals were recorded in small pocket-books, held by each of the observers, who very soon learned to code their observations and to make their entries without looking up from the ground. For this reason it was essential that the field notes were transcribed as soon as possible after each count. This was done during a daily noon break, and each evening.

Because of limitations in the overall period for which the helicopter was available for counting, it was not possible to

confine the activity to the most suitable times of the day. It was necessary to continue virtually throughout each day, with only the necessary refuelling stops and resting periods.

When large herds of impala or other species were encountered, the helicopter simply hovered overhead until a reliable tally for the herd had been obtained. Generally speaking however, it was possible to conduct the counting without even slowing down.

4.2.2. Results.

The results of the various counts conducted from a helicopter are shown in Table 5.

4.2.3. Discussion.

The helicopter provided the answer to only some of the problems encountered with the use of a fixed-wing aircraft. However its advantages are undoubtedly enormous.

For instance, it enabled the operation to be slowed down for the counting of large herds - even to the extent of being able to remain stationary in the hover position while a herd was counted completely. The "bubble" in which the passengers are seated also eliminated the error, described by Pennycruick (1969), created by the blind spot beneath the fixed-wing aircraft, where it is impossible to see anything. The extent of this "spot", which is in reality of course a strip, may amount to up to 7% or 8% of the total area counted, depending on the height above the ground and the width of the strip being counted. The technique employed in this earlier method of counting did not permit this blind spot

Table 5. Results of aerial counts of impala in Mkuzi Game Reserve obtained by the use of a helicopter in successive years from 1970 to 1978 (all data obtained from unpublished reports in Natal Parks Board files). The count for 1977 was incomplete.

Date of count.	Number counted.		Authors.
	Mkuzi	Nxwala	
May 1970	7 319	1 706	J. Vincent.
August 1970	6 495	1 214	J. Vincent.
September 1971	3 947	846	P. M. Hitchins.
July 1972	7 389	2 115	P. M. Hitchins.
July 1973	4 467	972	A. M. Whateley.
July 1974	3 637	2 330	P. M. Brooks and A. M. Whateley.
July 1975	5 795	2 414	A. M. Whateley and W. D. Densham.
July 1976	4 660	2 543	A. M. Whateley et al.
August 1978	8 030	2 485	W. D. Densham and P. S. Goodman.

to be covered, for the strip was not repeated on the return leg of a flight: there was no overlap.

Mence (1969) listed some of the psychological problems associated with aerial counting, amongst which was physical discomfort. In a fixed-wing aircraft it is not always easy to relieve any discomfort arising from one or another source, but in a helicopter, which is able to land without specialised facilities, such sources can often be eliminated or the effect reduced. One of the greatest advantages is being able to "drop down" for a rest at any time. However, one factor common to both types of counting, and which cannot be eliminated by any means other than a change of personnel, is airsickness. It is not always desirable or convenient to change the observer team during a count.

It was just this problem that was encountered during the helicopter count of 1971, when three separate observers suffered from the ailment, and the count itself was deemed very unsatisfactory for this reason. In each case a change meant a period of familiarisation during which efficiency was substantially reduced, and this was followed by nausea, when counting ceased altogether (Hitchins, pers. comm.).

A colleague, Mr. P.M. Hitchins, and I had all but perfected the technique of counting from a helicopter during some 70 hours of flying on this task in 1970. when my transfer to administrative duties in 1971 necessitated using new observers, all of whom, as has been described, suffered from nausea. The situation improved again in 1972 and in subsequent years, when observers used did not suffer from airsickness. This problem is reflected in the results shown in Table 5.

The most serious disadvantages of using a helicopter for census work is the expense. It cost, on an average, about R100 per hour to operate the machine that was used. This figure has been based on commercial rates of hire. To count all of Mkuzi Game Reserve and Nxwala required about 15½ hours in 1970 at a cost of R1550 and 14 hours in 1975 at a cost of R1400. This, compared to other methods, is clearly uneconomic, so that any other technique which achieves a reasonable degree of accuracy would be preferable.

Lamprey (1964) mentioned that impala, along with waterbuck (Kobus ellipsiprymnus), are too difficult to see from the air for a complete count to be made. Experience with impala in the study in Mkuzi supported this contention, but there was unfortunately no means of quantifying the error, other than by making comparisons with other methods of counting. The psychological reaction on the part of an observer with any experience in a helicopter to any suggestion that the results may be inaccurate, is indignation, for a certain degree of confidence in the counting method is achieved. This is purely personal and subjective however. It can also be a dangerous and erroneous misconception, for on numerous occasions whole herds were seen at the last moment before they disappeared from view beneath the aircraft, or were only observed because one individual out of many was spotted through the tree canopy. A measure of the counting error using a helicopter has been established by Brooks (1978) and will be discussed in a later section.

One of the major sources of error in counting from the air is the origin of the light source and its orientation in relation to the flight path and direction of observation. Graham and Bell

(1969) discussed this question in relation to the position of the sun, and concluded that counting should ideally take place when the sun is at an angle of between 15^{o} and 70^{o} from the horizontal. At the same time the count should be so planned that the animals are always observed in reflected light, i.e. when the light source (usually the sun) is behind the observer. This obviates the tiring effects of glare, and improves the contrast between the subject and the background, rendering the former more visible.

Again for economic reasons, to have confined the counting to one side of the aircraft only, to the ideal times of the day, and to only one direction on the flight path, would have proved quite impractical. The effect of glare when the sun was low - and on occasions even when it was high in the sky - was such that observation through the perspex "bubble" of the helicopter was extremely trying. These factors then, militate against accurate counting, even from a helicopter. The results achieved by this method cannot therefore be considered entirely accurate.

As has been described, the technique used in the aerial censussing was a series of parallel flight paths, with the two observers being alternately responsible for the strip counted on the previous run. This meant that there was very little chance of counting any one group of animals twice, particularly since none of the counting blocks was so large that it was not possible to recall the locality and size of a particular group on the return run. Where any doubt or possibility existed that a group had already been counted, the group was not included in the count. The results therefore are a true minimum count.

It could be argued that, because counting took place over

a period of more than one day, an inaccuracy might have been introduced by the movement of impala overnight. The same could logically be said of the fact that animals could have moved between counting blocks during the course of the count. However it was necessary to make the assumption that any movement, either overnight or between blocks, was random, and that as many animals moved into an area as moved out of it. One weakness in this assumption is that movements to and from water had of necessity to be fairly extensive, and it is possible that any such movement could be restricted to mornings or afternoons only, when impala were found to be most active. On the other hand, other observations (Chapter 3.2.) indicated that impala do not drink every day, and as many could have been counted in the vicinity of water as on the "home range". Thus the possibility that there may have been bias in the counting was discounted.

Finally, it is necessary to comment on the psychological effects of prolonged counting. Mence (1969) reviewed some of the problems of this nature that are associated with aerial censussing. Most of those mentioned by him can be overcome by experience, but that which probably causes the most trouble is the need for prolonged concentrated effort. This results in both mental and physical fatigue, but it was found that one simple way to overcome it was for the pilot to "overshoot" at the end of each run by a short distance, before making the turn. This meant that there was a brief period, perhaps amounting to 15 or 20 seconds, between successive runs, when the observers could relax and take their minds off the task of counting. This procedure, together with the need to land for refuelling every two or three hours, was found in my own experience to be quite adequate as a means of avoiding mental fatigue.

4.3. Road strip sample count.

4.3.1. Method.

The sampling technique employed was that used by Lamprey (1964) and also described by Teer et al (1965) and Hirst (1969a). It is based on a fixed visibility profile, and whilst Lamprey calculated the area of the sample strip beforehand, the other authors who are cited used the mean visibility distance along the cruise line as half of the mean sample strip width for calculation of the area sampled. The effective sample area should be approximately the same in the two cases.

A number of roads throughout Mkuzi Game Reserve were selected for transect purposes; they traversed a wide diversity of habitat types, considered to be representative of the reserve as a whole. The total distance covered by these transects was 98,84 km (59,55 miles). (All measurements were originally made in the English system, but have been concerted to metric equivalents). Some of these roads were simply administrative tracks - in a few cases no longer used for any other purpose than that of the present study and since closed permanently, whilst most of the distance was on tourist roads. The total distance was divided into 16 routes, which averaged 5,9 km, with a range from 3,2 km to 10 km (see Figure 6).

During the plotting of the visibility profile, the vehicle was stopped every 161 m (0,1 mile) and a reading taken. In order to obviate subjectivity, care was taken not to look right or left for the last few metres before stopping. The direction

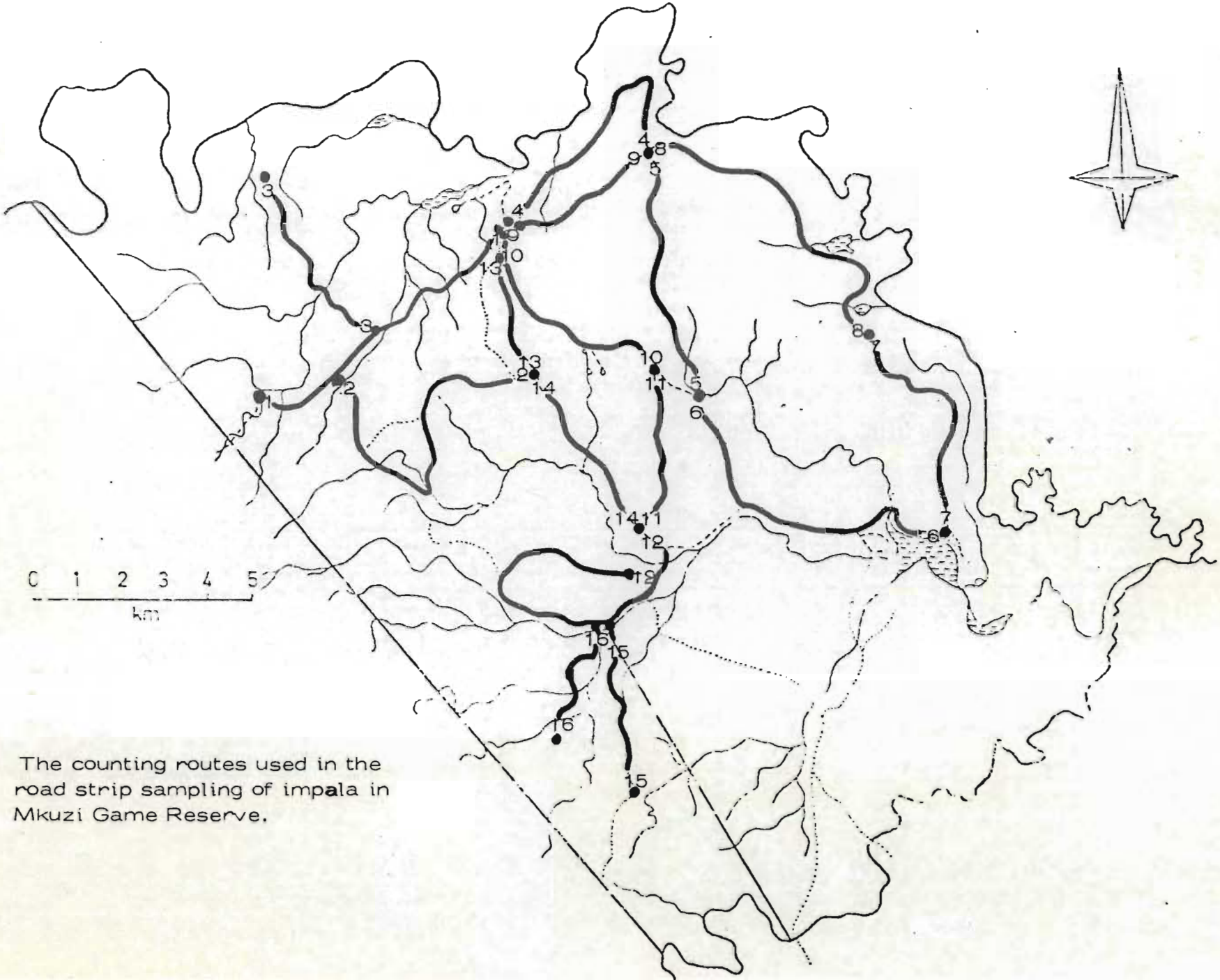

Figure 6. The counting routes used in the road strip sampling of impala in Mkuzi Game Reserve.

in which the measurement was taken was determined by sighting along a line across the rear end of the vehicle. A point on this line, on either side of the road, was then estimated as being the limit, beyond which distance an impala would disappear from view. In some cases this was simple, due to the intervention along the chosen line of a patch of thick bush. In only a very few instances was there any doubt in my mind as to the point of the limit of visibility.

The distance to this point was measured from the middle of the road, initially by means of a steel tape, and later simply by pacing it and checking occasionally with the tape. Later it was decided to use a rangefinder to determine the distance and again, checking at random with the steel tape ensured reasonable accuracy throughout. The original plotting of the visibility profile was carried out in June 1970, and periodic checks of various routes in both the winter and the summer months, were made throughout the study. Another complete profile was plotted in December 1970, as it was suspected that both seasonal and temporal changes might be revealed, because of changes in foliage density and grass cover and height.

During the course of each actual census, which occupied a total period of four days, every one of the routes was traversed in a Land Rover at an average speed of about 25 km/h, twice per day. The first census each day was started at sunrise, and the second as nearly as possible to that time of the afternoon that ensured completion of the transect at sunset. The actual finishing time depended largely on the number of observations made, and therefore on the number of stops that were necessary; on only two occasions was this time more than half an hour from sunset - both after that time, and just at dusk.

The time of sunset and sunrise was determined for each day by reference to the standard times detailed in Anon. (1957).

The speed of approximately 25 km/h was found to be optimum for one person to attend to the driving, as well as to observe impala within the visibility profile on both sides of the road. Certain conditions, such as thicker vegetation, necessitated a slower cruising speed, which was always in fact adapted to the prevailing situation.

The observer was equipped with a pair of binoculars (in this case with a magnification of 12 x 50, although a less powerful pair would have sufficed), and a pen and clipboard containing a supply of forms of the type shown in Figure 7. The purpose of this form was not only to record the number of individuals seen and their point of observation by reference to the odometer reading, but also to record the size of the herds, and their age and sex composition.

Naturally, there were many instances in which the entire herd was not counted for the reason that, when first seen, part of it was not visible to the observer. It was extremely difficult to remain unbiased in such cases, by not counting those individuals which were, for example, behind a bush to begin with, but which appeared whilst the rest of the herd was being counted. Nevertheless every effort was made to avoid this source of bias, which would have resulted in an overestimate of the population.

At the start of each route the odometer reading was recorded, as was the time. Where two routes were contiguous, the odometer reading at the start of the second route was of course

ROUTINE DATA SHEET

Road strip counts - Hide counts.

Route nos..... Date.....

Start at .....hrs, finish at.....hrs. Total time.....

Mileage	Route no./Time	Adult males	Adult females	Immature males	Juvenile males	Juvenile females	Juvenile unsexed	Unclassified	Total

Figure 7. Specimen field data sheet used in the road strip sampling of impala in Mkuzi Game Reserve.

the same as that at the end of the first; in those cases where this was not so, the reading was also taken at the end of the route.

Upon each sighting of impala, the vehicle was stopped and the ages were determined, and checked if possible, before being recorded. Recording was done on the prescribed form against the relevant odometer reading. Where a herd was spread over such an area as to be embraced by more than one such reading, the various figures were bracketed together, and all were treated as a single herd for the purpose of analysis. Each distinct herd however, was recorded separately and where it was clear that individuals from a particular herd were not all visible, this was noted. The reason for recording the odometer reading in each case was so that, by reference to a habitat map, upon which the distances were marked, it was possible to determine, on subsequent analysis, the habitat type occupied by each herd at the time. This information was used for ascertaining seasonal distribution changes and habitat preferences, as well as for census and density determination purposes.

A total of 23 sample censusses was carried out in this fashion during the three year study period. During the period from February 1970 to January 1972, December 1971 was the only month in which a sample was not obtained.

4.3.2. Stratification.

In Chapter 3 the habitat preferences and requirements of impala were considered, and it was shown that there is a distinct preference for open to closed woodland. Impala tend

to shun thicket, particularly in Mkuzi, where this consists mainly of Acacia luederitzii and Euclea divinorum, neither of which is a preferred food plant, and beneath which there is normally a very sparse ground cover. Furthermore, in Mkuzi, the impala make no use at all of the upland grassveld on the tops of the Lebombo mountains, with their shallow soils and largely xerophytic vegetation.

For the purpose of population sampling Mkuzi Game Reserve was therefore stratified on the basis of the physiognomic vegetation types. This was carried out as follows:

Nil. Impala completely absent for most if not all of the year. Restricted to the limited area of grassveld on the top of the Lebombo mountains. 2 006 ha (8,0% of the reserve).

Low. (i) Combretum apiculatum open woodland on the upper slopes of the Lebombo mountains, above about 122 m (400'), where the soils are shallow and food value of the ground cover poor.
(ii) Acacia luederitzii/Euclea divinorum thicket on Recent sands in the lowlands, but excluding the smaller thicket patches in the drainage lines of the foothills, which have a different composition.
(iii) Riverine woodland in the Mkuze and Msunduze river gorges.
(iv) Xeric sand forest.
Total stratum area: 6 191 ha (24,7% of the reserve).

Medium. (i) Combretum apiculatum open woodland below about 122 m (400'), where elements of other

associations are present due to better soils.
(ii) Drainage line thickets on the soils derived from Lebombo volcanics. Contain Acacia woodland elements.
(iii) Riverine gallery forest along the Mkuze river.
Total stratum area: 7 412 ha (29,6% of the reserve).

High. (i) All Acacia open to closed woodlands, except A. luederitzii thickets, and including A. nigrescens open woodland, A. tortilis, A. nilotica and A. gerrardii woodland associations.
(ii) All broadleaved woodlands on Recent sands, except xeric sand forest.
Total stratum area: 9 472 ha (37,8% of the reserve).

The dry season water distribution may to some extent determine impala habitat preferences, for at the end of winter there is frequently water present only at the two artificially supplied waterholes (Bube and Msinga) in the middle of the reserve. However, since the impala is a highly mobile species, and no point in the reserve is more than about 10 km from the water, this factor was not considered in mapping the strata. No point in the high density stratum is more than about 6 km from the water, and most of it is less than 3 km from it.

In fact, during the course of this study, in addition to the water supplied at Bube and Msinga, there was also water in the Mkuze gorge and, for most of the time, in a small pan in the

south-eastern corner of the reserve.

The distribution of the three strata used in the population estimation is shown in Figure 8.

4.3.3. Results.

4.3.3.1. Visibility profile.

Tables 6 and 7 show the data obtained from two determinations of the visility profile - one in winter (June) and the other in summer (December). They also show the total area on each of the routes which was visible from the cruise line. The difference in total area between the two determinations was negligible: a mere 2,68 ha, or the difference between 1 267,88 ha in June and 1 265,20 ha in December. This could have been attributable to sampling error and it is not significant. The proportion of the inhabited area of the reserve that was visible from the cruise lines was 6,78%.

It was thought that the visibility would decrease in summer, with the comparatively longer grass and greater density of woody vegetation. However this was not the case, and the difference between winter and summer was very small - if it existed at all. This can be attributed to the facts that (a) the grass did not anywhere reach such a height that it obscured the view of impala from the cab of a Land Rover, and (b) the vegetation contained only a comparatively small element of deciduous species. In fact, the generally heavy utilization of the habitat rendered the grass over most of the impala range seldom tall enough to obscure an impala that was lying down, at least for the duration

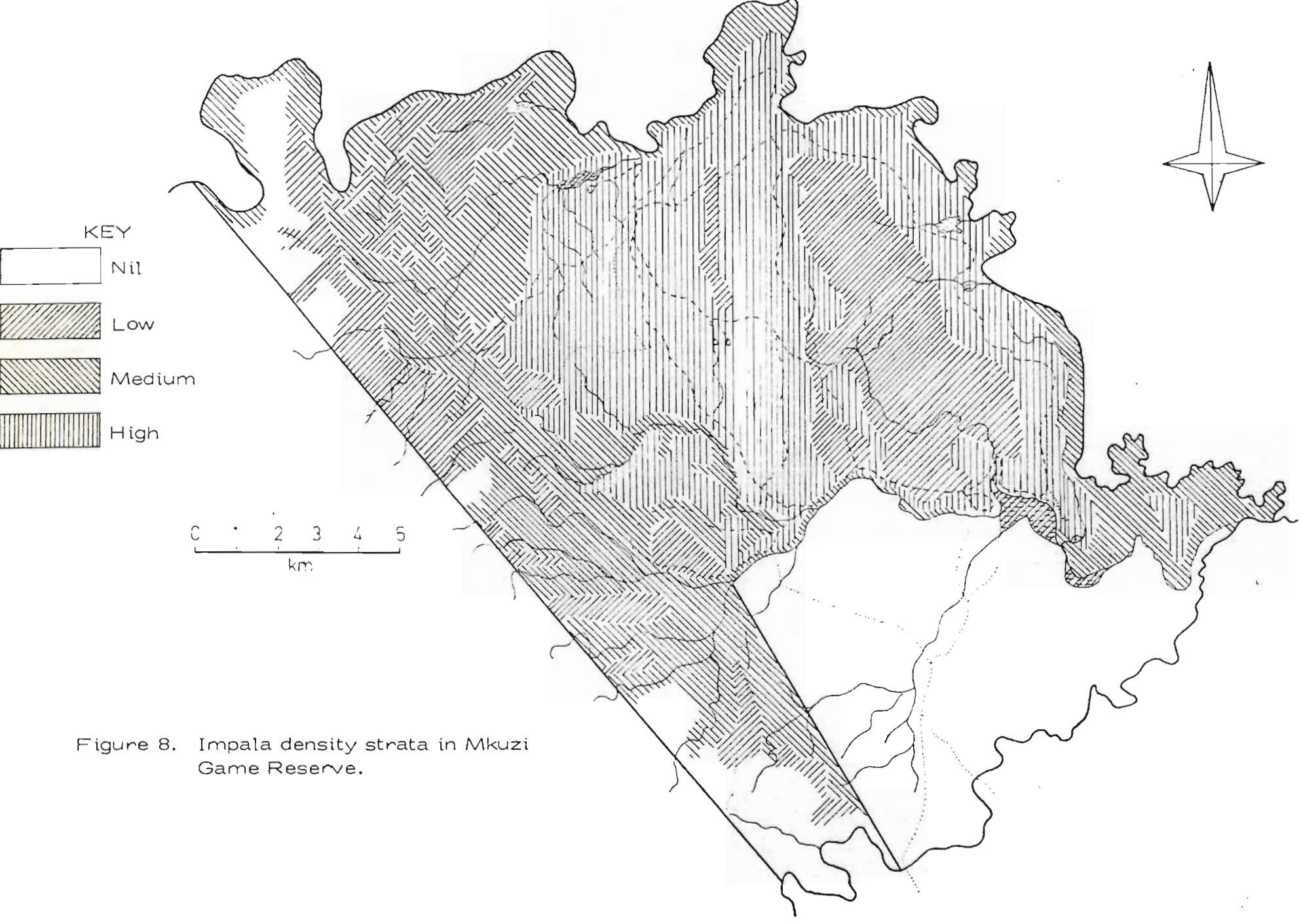

Figure 8. Impala density strata in Mkuzi Game Reserve.

Table 6. Data used in the construction of a visibility profile for each of the selected counting routes in Mkuzi Game Reserve in June 1970.

Route number	Distance (km)	Average visibility (metres)			Area visible (hectares)
		Left	Right	Total	
1	8,05	81,87	62,42	144,29	116,15
2	8,37	87,26	72,81	160,07	133,98
3	4,67	117,47	114,36	231,83	108,26
4	6,44	37,76	43,65	81,41	52,41
5	4,99	104,03	52,67	156,70	78,19
6	10,46	38,80	65,84	104,64	109,45
7	5,95	44,26	47,00	91,26	54,30
8	8,37	44,32	59,07	103,39	86,54
9	3,70	56,14	32,55	88,69	32,82
10	5,31	54,74	49,62	104,36	55,42
11	5,31	46,23	59,77	106,00	56,29
12	9,17	89,18	90,59	179,77	164,85
13	3,54	69,46	78,51	147,97	52,38
14	4,99	84,76	88,85	173,61	86,63
15	3,22	30,81	95,10	125,91	40,54
16	3,70	46,72	60,44	107,16	39,65
TOTAL	96,24	1 033,81	1 073,25	2 107,06	1 267,88
MEAN		64,61	67,08	131,69	

Table 7. Data used in the construction of a visibility profile for each of the selected counting routes in Mkuzi Game Reserve in December 1970.

Route number	Distance (km)	Average visibility (metres)			Area visible (hectares)
		Left	Right	Total	
1	8,05	83,42	60,61	144,03	115,94
2	8,37	83,11	74,26	157,37	131,72
3	4,67	122,50	119,03	241,53	112,79
4	6,44	36,64	42,12	78,76	50,72
5	4,99	103,71	52,88	156,59	78,14
6	10,46	36,21	64,38	100,59	105,22
7	5,95	45,76	46,79	92,55	55,07
8	8,37	44,58	58,61	103,19	86,37
9	3,70	55,77	33,14	88,91	32,90
10	5,31	57,25	46,15	103,40	54,91
11	5,31	46,56	58,91	105,47	56,00
12	9,17	93,27	91,37	184,64	169,31
13	3,54	65,16	74,21	139,37	49,34
14	4,99	84,32	89,47	173,79	86,72
15	3,22	30,72	99,26	129,98	41,85
16	3,70	44,95	58,22	103,17	38,20
TOTAL	96,24	1 033,93	1 069,41	2 103,34	1 265,20
MEAN		64,62	66,84	131,46	

of the study. Where this did occur, it implied that the grass was unpalatable, e.g. Bothriochloa insculpta, and therefore not used even in winter.

In recent years, due partly to population management but mainly to higher rainfall, the grass has become particularly tall and dense in parts, rendering the observation of impala a great deal more difficult.

After stratification had been applied to the data, the area of ground actually visible in each stratum, together with this figure expressed as a percentage of the total area represented by each stratum in the entire study area, are shown in Table 8. The visible area used is the mean of that determined in the two calculations of the visibility profile (See Tables 6 and 7).

4.3.3.2. Sample counts.

Counts by the visibility profile method were carried out at the rate of one per month from February 1970 to January 1972, with the exception of December 1971. In addition to these 23, a further three counts were carried out, which embraced all the sampling routes, but which lasted only one day each and involved only one count on each route. These counts were done in May, June and August 1972. Their limited duration meant moreover, that no consideration was given to the time of day, for most of a day was required for the exercise. These counts were not used in density calculations, but the results were used for comparison with the population structure determined from other samples.

The average time spent in traversing all the 16 routes was

Table 8. The area (in hectares) represented by each density stratum in the visibility profile, and this area expressed as a percentage of the total area of Mkuzi in the relevant stratum.

Stratum	Visible area (hectares)	Total area (hectares)	% visible
Nil	-	2 006	-
Low	66,93	6 191	1,08
Medium	309,62	7 412	4,18
High	889,99	9 472	9,40
Total	1 266,54	25 081	5,49*

*Does not take into account the area where no impala are present, i.e. nil stratum.

about 5h 40m, with a range from 5h 5m to 6h 10m, depending upon the total number of animals or groups seen, and the consequent number of vehicle stops and entries that were necessary.

This technique of road strip sampling was based on the assumption that the distribution of impala was random in relation to the roads, and that there was no particular bias in sampling toward one or another age class or sex due to its preference or otherwise for the vicinity of roads.

More serious than this form of possible bias was the fact that no amount of care could have eliminated the error caused by the inherent shyness and nervous disposition of impala and by their natural and predictable tendency to move away from the roadsides on the approach of a vehicle. This was a "negative factor", but on the other hand there was the "positive" one, created when a large herd was encountered, and which resulted in a tendency to overestimate the number of animals. Under these circumstances, and because herds frequently moved across the road in front of the vehicle, more impala were counted than would have been visible at the time of first sighting them, or if they had remained stationary whilst they were being observed. Although every effort was made to eliminate this error, I often tended to give a number of animals the "benefit of the doubt" and to include them in the sample in an effort to neutralise the negative error. Naturally, no measure of the accuracy or otherwise of this attempt at compensation was possible, and the factor remains a major source of possible error in the census.

The results of all the counts are shown in Table 9, and in Figure 9 they are shown graphically in relation to the rainfall figures at the reserve headquarters. Figure 10 illustrates the same data, but with the number of animals seen each month expressed as a percentage of the total for the year.

The means, standard deviations of the means, and 95% confidence intervals, of the numbers actually sampled in 1970 and 1971 and in both years together, are as follows:

	Mean	Standard deviation	95% confidence intervals
1970	2 386	468,0	± 297
1971	2 387	314,7	± 211
Both	2 387	393,1	± 170

4.3.3.3. Population estimates.

Each of the 16 counting routes was divided into sections according to the predetermined density strata, and the number of animals recorded in each month in each stratum was used to calculate the density and total population for each of the two years. The results are shown in Tables 10 and 11, in which n is the number of animals sampled, a is the area sampled in each stratum, and A is the total area of the stratum in the reserve.

An analysis of variance was carried out separately for each year in an attempt to show that the density strata used were in fact meaningful. These analyses are shown in Table 12(a) and (b), from which it is clear that the stratification is highly significant, with $P<0,005$. Table 13 also shows how the stratification is meaningful, with the difference between the calculated and expected populations (assuming random distribution

Table 9. The number of impala recorded during morning and afternoon counting sessions on each of the monthly sample counts in Mkuzi Game Reserve, from February 1970 to January 1972, and on each of the three one-day counts in 1972.

Month	Number seen			Mean
	Morning	Afternoon	Total	
February 1970	1 662	1 214	2 876	1 438
March	1 253	1 052	2 305	1 153
April	698	1 733	2 431	1 215
May	943	1 217	2 160	1 080
June	972	1 077	2 049	1 025
July	1 043	909	1 952	976
August	936	788	1 724	862
September	1 109	1 003	2 112	1 056
October	1 111	1 135	2 246	1 123
November	956	1 559	2 515	1 258
December	1 278	1 592	2 870	1 435
January 1971	1 765	1 633	3 398	1 699
February	1 475	1 206	2 681	1 341
March	1 077	1 494	2 571	1 286
April	931	1 571	2 502	1 251
May	919	1 132	2 051	1 026
June	1 416	968	2 384	1 192
July	1 201	1 053	2 254	1 127
August	1 118	924	2 042	1 021
September	1 207	852	2 059	1 030
October	1 290	808	2 098	1 049
November	1 164	1 474	2 638	1 319
December	-	-	-	-
January 1972	2 191	790	2 981	1 491
May 1972				1 185
June				869
August				800

Note: The three one-day counts in 1972 each covered all the routes once only, and each occupied most of the day.

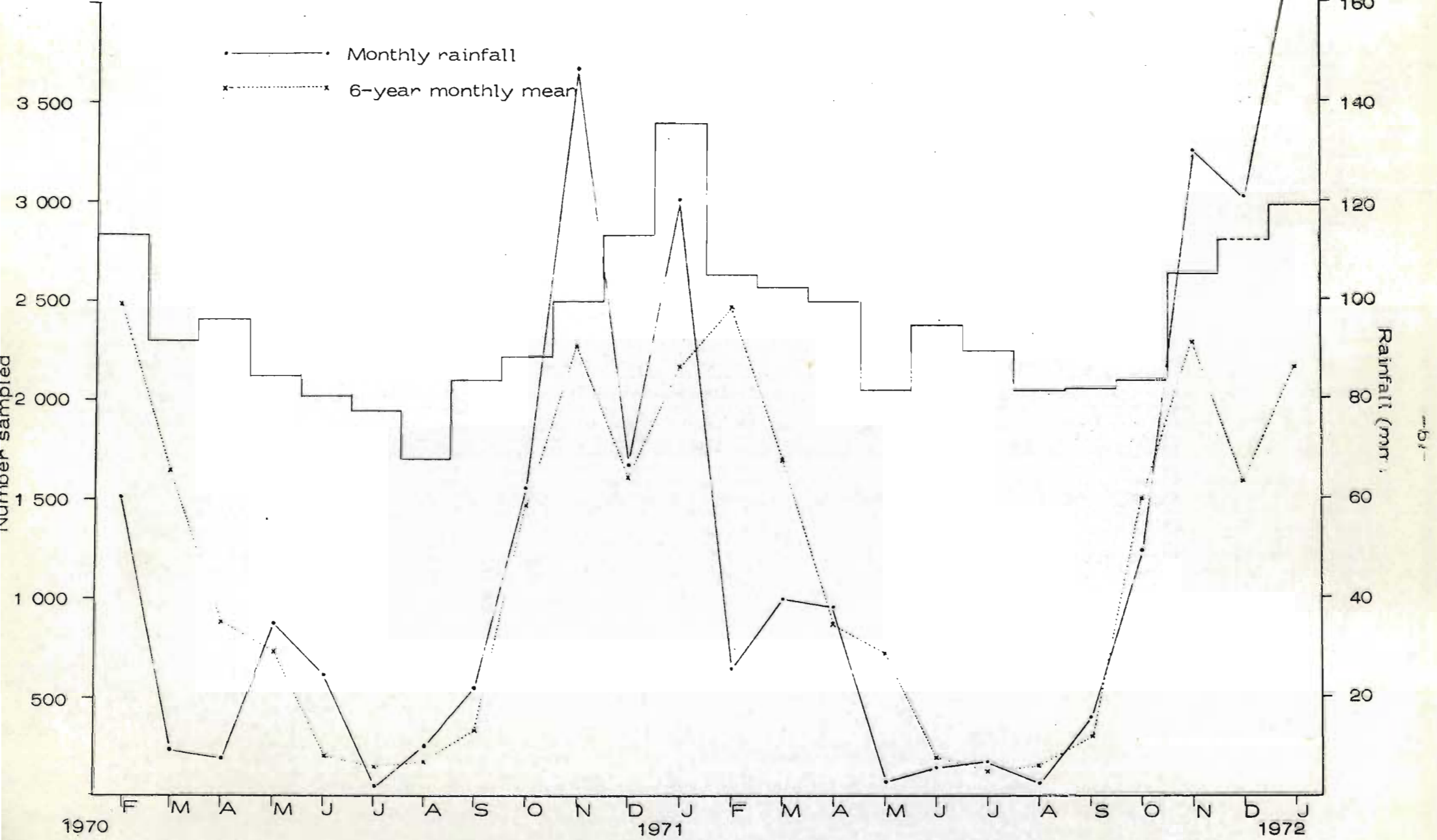

Figure 9. The number of impala seen in each month of the road survey (histogram), together with the rainfall data for Mkuzi Game Reserve.

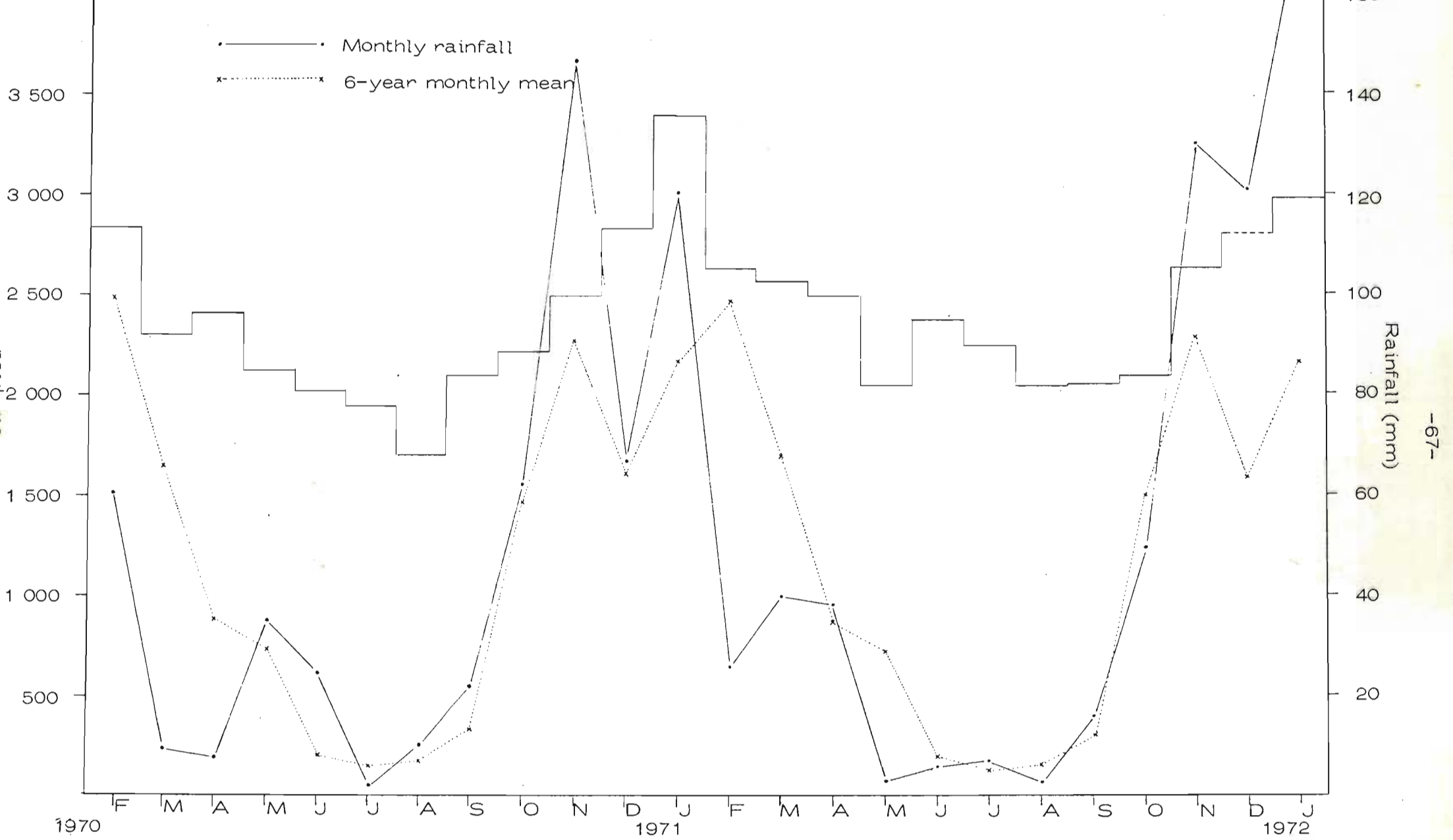

Figure 9. The number of impala seen in each month of the road survey (histogram), together with the rainfall data for Mkuzi Game Reserve.

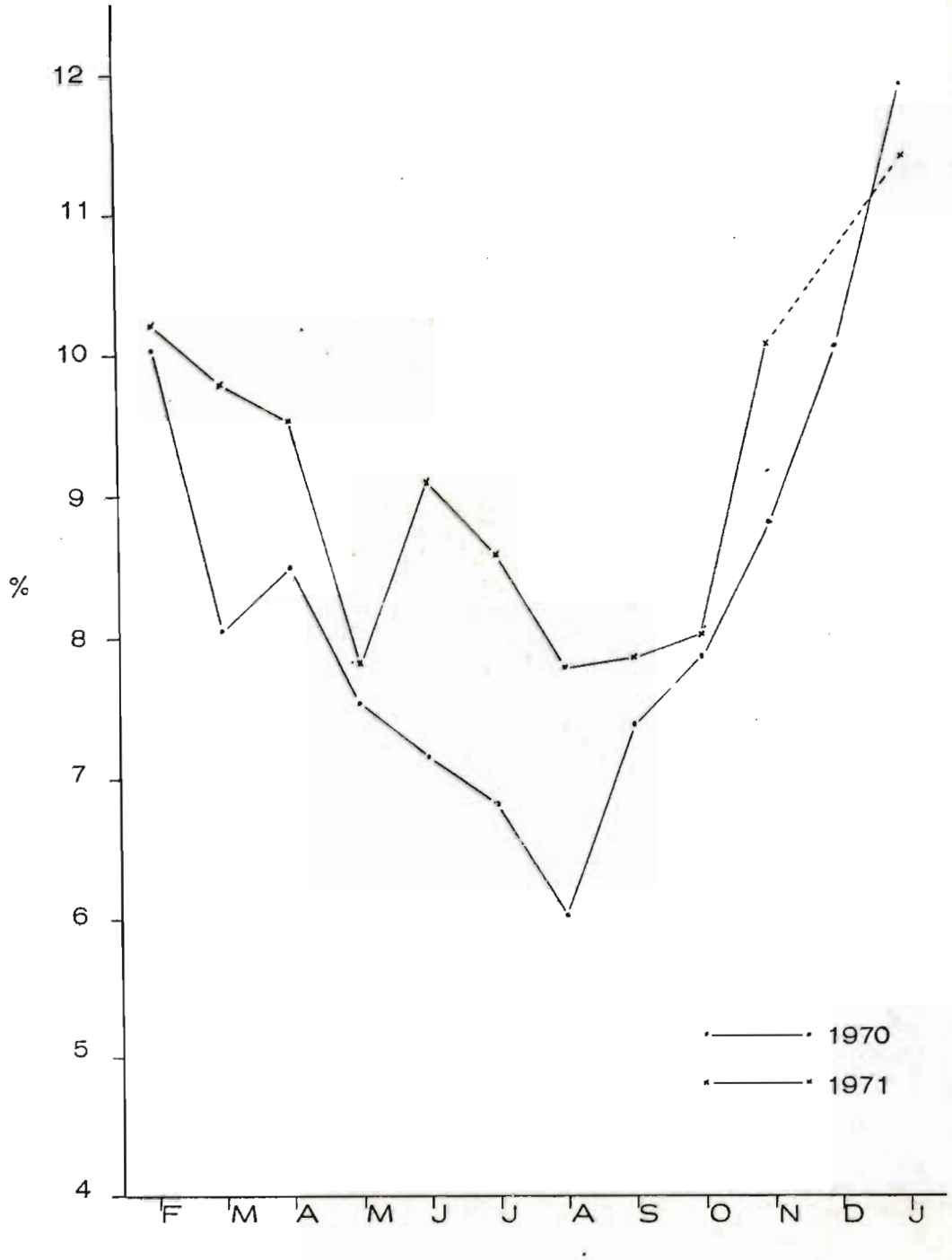

Figure 10. Number of impala seen during the road strip sampling in each month of the year expressed as a percentage of the total seen in that year.

Table 10. Calculation of the impala population in each stratum in each month during the 1970 sampling.

Month	Stratum	No. of animals seen (n).	Density (n/a)	Population estimate(nA/a)	Total populat estimate
February	High	1 203	1,352	12 803	19 594
	Medium	218	0,704	5 219	
	Low	17	0,254	1 572	
March	H	838	0,942	8 919	18 448
	M	286	0,924	6 847	
	L	29	0,433	2 682	
April	H	978	1.099	10 409	17 728
	M	213	0.688	5 099	
	L	24	0,359	2 220	
May	H	853	0,958	9 078	16 295
	M	201	0,649	4 812	
	L	26	0,388	2 405	
June	H	788	0,885	8 387	15 363
	M	218	0,704	5 219	
	L	19	0,284	1 757	
July	H	726	0,816	7 727	15 562
	M	223	0,720	5 338	
	L	27	0,403	2 497	
August	H	649	0,729	6 907	13 994*
	M	184	0,594	4 405	
	L	29	0,433	2 682	
September	H	885	0,944	9 419	14 472
	M	157	0,507	3 758	
	L	14	0,209	1 295	
October	H	927	1,042	9 866	15 797
	M	178	0,575	4 266	
	L	18	0,269	1 665	
November	H	1 092	1,227	11 622	16 761
	M	149	0,481	3 567	
	L	17	0,254	1 572	
December	H	1 260	1,416	13 410	18 490
	M	162	0,523	3 878	
	L	13	0,194	1 202	
January	H	1 524	1,712	16 220	21 506
	M	159	0,514	3 806	
	L	16	0,239	1 480	
Mean					17 001

Area of each stratum sampled (a)

High	889,99 ha
Medium	309,62 ha
Low	66,93 ha

Total area of each stratum (A)

High	9 472 ha
Medium	7 412 ha
Low	6 191 ha

* 1 252

Table 11. Calculation of the impala population in each stratum in each month during the 1971 sampling.

Month	Stratum	No. of animals seen (n).	Density (n/a)	Population estimate (nA/a)	Total populat estimate
February	High	1 044	1,173	11 107	20 770
	Medium	260	0,841	6 233	
	Low	37	0,554	3 430	
March	H	1 091	1,226	11 611	19 638
	M	146	0,472	3 495	
	L	49	0,732	4 532	
April	H	1 019	1,145	10 845	18 593
	M	200	0,646	4 788	
	L	32	0,478	2 960	
May	H	866	0,973	9 217	15 583 *
	M	123	0,397	2 944	
	L	37	0,553	3 422	
June	H	1 025	1,152	10 909	16 141
	M	149	0,481	3 567	
	L	18	0,269	1 665	
July	H	949	1,066	10 097	15 797
	M	157	0,507	3 758	
	L	21	0,314	1 942	
August	H	870	0,978	9 264	14 116
	M	133	0,430	3 187	
	L	18	0,269	1 665	
September	H	800	0,899	8 514	15 871
	M	203	0,656	4 860	
	L	27	0,403	2 497	
October	H	801	0,900	8 525	16 244
	M	222	0,717	5 314	
	L	26	0,388	2 405	
November	H	1 112	1,249	11 835	18 299
	M	185	0,598	4 429	
	L	22	0,329	2 035	
January	H	1 231	1,383	13 101	21 519
	M	228	0,736	5 458	
	L	32	0,478	2 960	
Mean					17 506

Area of each stratum sampled (a)

High	889,99
Medium	309,62
Low	66,93

Total area of each stratum (A)

High	9 472
Medium	7 412
Low	6 191

* 2 148 animals removed by capture.

Table 12(a). Analysis of variance of sampled populations between sampling units (months) and strata for 1970 data.

Source of variation	Sum of squares	Degrees of freedom	Mean square
Strata	6 220 808	2	3 110 404
Error	712 780	33	21 599
Total	6 933 588	35	

$$F = \frac{3\ 110\ 404}{21\ 599} = 144{,}00$$

$P < 0{,}005$

Table 12(b). Analysis of variance of sampled populations between sampling units (months) and strata for 1971 data.

Source of variation	Sum of squares	Degrees of freedom	Mean square
Strata	5 767 888	2	2 883 944
Error	211 193	30	7 040
Total	5 979 080	32	

$$F = \frac{2\ 883\ 944}{7\ 040} = 409{,}65$$

$P < 0{,}005$

Table 13. Comparison between the calculated and expected populations (assuming random distribution) of impala in each month and in each stratum in Mkuzi in 1970 and 1971.

Month	Stratum	1970		1971		Expected populat	
		Calculated population	% of total	Calculated population	% of total	1970	1971
	High	12 803	65,3	11 107	53,5	8 043	8 526
February	Medium	5 219	26,6	6 233	30,0	6 671	6 671
	Low	1 572	8,0	3 430	16,5	5 257	5 573
	High	8 919	48,3	11 611	59,1	7 573	8 061
March	Medium	6 847	37,1	3 495	17,8	5 925	6 308
	Low	2 682	14,5	4 532	23,1	4 950	5 269
	High	10 409	58,7	10 845	58,3	7 278	7 632
April	Medium	5 099	28,8	4 788	25,8	5 694	5 972
	Low	2 220	12,5	2 960	15,9	4 756	4 989
	High	9 078	55,7	9 217	59,1	6 689	6 397
May	Medium	4 812	29,5	2 944	18,9	5 234	5 005
	Low	2 405	14,8	3 422	22,0	4 372	4 181
	High	8 387	54,6	10 909	67,6	6 306	6 626
June	Medium	5 219	34,0	3 567	22,1	4 935	5 184
	Low	1 757	11,4	1 665	10,3	4 122	4 331
	High	7 727	49,7	10 097	63,9	6 388	6 485
July	Medium	5 338	34,3	3 758	23,8	4 999	5 074
	Low	2 497	16,0	1 942	12,3	4 175	4 238
	High	6 907	49,4	9 264	65,6	5 745	5 795
August	Medium	4 405	31,5	3 187	22,6	4 495	4 534
	Low	2 682	19,2	1 665	11,8	3 754	3 787
	High	9 419	65,1	8 514	53,6	5 941	6 515
September	Medium	3 758	26,0	4 860	30,6	4 648	5 098
	Low	1 295	8,9	2 497	15,7	3 883	4 258
	High	9 866	61,8	8 525	52,5	6 483	6 668
October	Medium	4 266	26,7	5 314	32,7	5 072	5 218
	Low	1 665	10,4	2 405	14,8	4 237	4 358
	High	11 622	69,3	11 835	64,7	6 880	7 512
November	Medium	3 567	21,3	4 429	24,2	5 384	5 878
	Low	1 572	9,4	2 035	11,1	4 497	4 909
	High	13 410	72,5			7 590	
December	Medium	3 878	21,0			5 939	
	Low	1 202	6,5			4 961	
	High	16 220	75,4	13 101	60,9	8 828	8 833
January	Medium	3 806	17,7	5 458	25,4	6 908	6 912
	Low	1 480	6,9	2 960	13,8	5 770	5 774
M.	High	10 397	61,1	10 456	64,8	6 979	7 186
Mean	Medium	4 685	27,6	4 367	21,8	5 461	5 623
	Low	1 919	11,3	2 683	13,4	4 561	4 697

The proportions of the total area represented by each stratum are:

High	41,05%
Medium	32,12%

over the whole reserve) highly significant in the high and low density strata, but less so in the medium stratum.

Thus in the high density stratum
in 1970, $t = 6,08$; d.f. = 11; and $P < 0,001$;
in 1971, $t = 12,39$; d.f. = 10; and $P < 0,001$.

and in the medium density stratum
in 1970, $t = -2,37$; d.f. = 11; and $P < 0,05$;
in 1971, $t = -4,63$; d.f. = 10; and $P < 0,005$.

and in the low density stratum
in 1970, $t = -10,00$; d.f. = 11; and $P < 0,001$;
in 1971. $t = -9,28$; d.f. = 10; and $P < 0,001$.

The mean and 95% confidence limits of the population were 17 001 $\pm$ 1 408 and in 1971 they were 17 506 $\pm$ 1 609.

4.3.3.4. Density.

The mean density over the whole inhabited portion of Mkuzi Game Reserve for the two years combined was 0,747 impala per hectare, or 74,7 per square kilometre. The highest single monthly density was of 1,712 impala per hectare, in the high density stratum in January 1971. The mean densities for each year were as follows:

1970	High	1,098 per hectare
	Medium	0,632 per hectare
	Low	0,310 per hectare
1971	High	1,104 per hectare
	Medium	0,589 per hectare
	Low	0,433 per hectare

Comparable densities of impala on other extensive ranges in Africa are shown in Table 14.

Table 14. Comparative densities of impala, expressed in animals per hectare, on extensive ranges in Africa.

Area	Density	Source
Tarangire	0,213	Lamprey (1964)
Lake Manyara	0,035	Watson (1965)
Lake Nakuru	0,090	Kutilek (1974)
Loliondo	0.003	Watson, Graham and Parker (1969)
Timbavati	0,351 - 0,586	Hirst (1969a)
Nairobi N.P.	0,043 - 0,060	Foster and Kearney (1967)
		Foster and McLaughlin (1968)
Kariba Dam	0,257 - 0,567 Mean: 0,324	Jarman (1971)
Kruger N.P.	0,046 - 0,158 Mean: 0,095	Pienaar (1963)
Kruger N.P.	0,102	Pienaar (1969)
Mkuzi Game Reserve	0,747	This study

4.3.4. Discussion.

4.3.4.1. Stratification.

The theorectical considerations of stratification have been discussed in some detail by Cochran (1963). The technique can be very usefully employed where it is possible to obtain distinct strata on one or another basis. The choice of the variable is one which must depend on circumstances. Generally speaking, as has been pointed out by Blankenship et al (1971), distinction between strata should be made on sound ecological principals, such as the vegetation type, provided that the population is dependent upon such factors. These authors reported on a switch from stratification on the basis of physiography to that using natural vegetation zones. The latter was considered to be more reliable, and has been shown to provide reduced error variance, and consequently greater precision.

In this study the vegetation was selected as the most suitable factor by which to distinguish strata. Hirst (1969a) used "habitat suitability", but abandoned stratification because of impracticability in his study area, where several ungulate species were sampled.

4.3.4.2. Sample census methods.

Hirst (1969a) discussed the "belt transect" sampling method, which is a modification of the basic "King strip census" (Leopold, 1933), and which has been used in one form or another by various authors (e.g. Kelker 1945, quoted in Hirst 1969a). He concluded, after experimenting with it in an open grassland area, that it was unreliable and consistently

gave an underestimate of the actual population. In woodland conditions particularly, the number of animals recorded within the predetermined "strip" is likely to be less than the actual number in the strip, and the method will therefore also result in an underestimate of the population.

On the other hand, the method used by Dasmann and Mossman (1962a), whereby the mean perpendicular distance from the cruise line to the observed animals is used to represent half the strip width, must (and, according to Hirst 1969a, did) overestimate the population. As long as it can be assumed that no individuals will be visible outside the predetermined visibility profile, then this latter is the maximum area which it is possible to sample. If however, the distance to each observation is measured, there will almost always be the "residual distance" between the farthest individual and the limit of visibility, unless that individual is situated at that limit. This residual distance is still being sampled. The effect will be a mean strip width somewhat less than the mean width calculated by the visibility profile method, and therefore a smaller effective total sampled area. After calculation, in which the sampled area is projected to the whole study area, this will theoretically result in an overestimate of the population.

The visibility profile method can be compared very closely with sampling in vegetation analysis. Here the botanist is usually concerned with a predetermined sample area, in the form of either a plot or a transect of known area. Because he is dealing with organisms that do not move, he can be assured of tallying all the individuals, and the only way of being reasonably sure of doing this with animals, particularly in woodland

conditions, is to record all those seen. Therefore the total area in which they will be visible from the cruise line must be determined.

Because there is a possibility that not all animals within the visibility profile will be seen, this method may result in an underestimate of the population.

4.3.4.3. Density.

Figures 9 and 10 demonstrate a distinct increase in the number of animals seen in Mkuzi Game Reserve during the summer months. This will be discussed in a later section, dealing with the distribution, as will the apparent changes in the concentrations of the various sex and age classes.

There is an apparent anomaly in the figures in 1971 (see Table 11), when the density in the "low" stratum exceeded that in the "medium" in March and May. This may be accounted for by the fact that the summer season of 1970/71 had a comparatively poor rainfall, and the veld conditions deteriorated earlier in the year. The impala were therefore forced to make use of normally unsuitable habitat such as thickets in search of browse.

The main population control programme took place in May 1971, which may also in part account for the anomalous density figures in that month, for animals would have been disturbed by the capture operations, in which a helicopter was used, and they would probably have taken refuge in thicket areas. The sample was taken almost immediately after capture.

The density of impala on the Mkuzi range, which averaged 0,747 per hectare for the two years combined, is higher than that for any other range in Africa. This is probably attributable to two factors, namely the lack of predators (Brooks 1975) and the restricted nature of the population's range. Habitat deterioration was apparent in 1971, so that stricter population reduction was consdered necessary.

4.3.4.4. General discussion.

In an experiment carried out by Brooks (1978) the efficiency of helicopter counting was assessed. In order to do this, the total numbers of all large mammal species were obtained in several counting blocks by means of a drive count involving about 75 counters in each of several defined areas. The main line of counters walked systematically through an area and recorded all animals that broke back through the line. At the same time, a number of other counters stayed just ahead of the main line, on the outer limits of each area, and recorded animals that left the area ahead of the line. The results obtained in this way were compared with those of helicopter counts carried out in the same way as has been described here.

Brooks' (1978) study area was Hluhluwe Game Reserve, which has more broken terrain but similar vegetation to Mkuzi with a mosaic of open and closed woodland and some thicket. The conditions for counting by helicopter are therefore much the same as those pertaining in Mkuzi Game Reserve.

The mean of 15 foot counts of impala in 10 different areas was 1 173, and of 17 helicopter counts in the same counting areas was 541,6. This gave a conversion factor

from results using the helicopter to the actual population obtained by ground counting of 2,17.

This conversion factor was then applied to the results of the separate helicopter counts in Mkuzi carried out in May and August 1970. As has been pointed out, the results obtained in 1971 were considered very unsatisfactory because of the airsickness of a succession of observers (Hitchins, pers. comm.). Application of the factor to the May count of 7 319 gives an estimate of 15 882 and to the August count of 6 495 one of 14 994. These are very close to the figures of 16 295 and 13 994 respectively obtained in the road strip sampling (see Table 10).

CHAPTER 5.

BEHAVIOUR

5.1. Introduction.

The individual behaviour patterns of impala have been well documented (Schenkel 1966a, 1966b, Leuthold 1970). Both these authors dealt with East African populations, but the behaviour is unlikely to differ to that of southern populations. Social behaviour, on the other hand can be expected to be quite different because of the seasonality of breeding in the south in contrast to year-round breeding in East Africa.

Social behaviour may be defined as the summation of interactions between individuals in a population. Several authors have concerned themselves specifically with social behaviour. Of these Schenkel (1966a, 1966b), Leuthold (1970), and Jarman and Jarman (1974) dealt with East African populations, whilst Dasmann and Mossman (1962a), Anderson (1972) and Mason (1976) discussed populations in southern Africa. Jarman (1974) categorised impala as a gregarious species with a number of behavioural characteristics in common with several other African animals, and Estes (1974) described impala as having an "intermediate" social organisation, with the characteristics of "medium-sized herds, clumped distribution, low density, sedentary."

Much of the social behaviour of impala is associated with

reproduction and, because breeding is seasonal in Mkuzi (Vincent 1972) and year round in East Africa (Kayanja 1969, Spinage 1973), it can be expected that behaviour will differ to some extent between the two regions. The aim of this aspect of the study in Mkuzi was therefore to record some of the behavioural characteristics of a seasonally breeding population.

The terminology used in this and subsequent chapters for the different age classes is as follows:

a. Juveniles. This is applied to animals up to 12 months of age, i.e. the young of the year. It was not possible to distinguish between males and females before about three months of age, at which stage the horns of males became evident. From the age of about nine months it became difficult to distinguish juveniles from older animals in the field unless they were standing next to each other.

b. Immature. This is applied to animals between 12 and 24 months old, i.e. yearling. Immature females were indistinguishable from older animals in the field, whilst the horn shape of males enabled them to be identified at least up to 23 months old in most cases. At this stage the horns of some of the more robust individuals were very similar to those of some of the older animals, so that from this age on all males except juveniles were classified together.

c. Adults. This class includes all animals over 24 months old, although in effect the field classification as adults included males over 23 months old and females over nine months old.

5.2. Methods.

The censussing technique enabled records to be maintained

of social behaviour. These records were supplemented by observations in localised study areas, more particularly on territorial behaviour, and by observations at waterholes.

The most detailed study, that on territorial behaviour, was carried out as follows:

Having established that the peak of territorial behaviour in 1970 occurred in the third week of May, a period of three days at that time in 1971 was spent in observing this behaviour in a small study area previously selected for the incidence of territorial males. This study area was situated along part of one of the counting routes which, during the survey in early May 1971, was seen to be occupied by a number of lone males apparently exhibiting territoriality. It was one of several such "concentrations" of lone males seen during that survey, and was selected for intensive study because of the comparative ease with which the animals could be observed.

The vegetation was predominantly open woodland dominated by Acacia nilotica, about two to three metres high. On one side this graded into A. luederitzii thicket, and on the other the A. nilotica gave way to more open woodland with A. nigrescens dominant. Visibility was about 400 m in this woodland, but less where the thicket intervened. A seasonal pan, dry at the time, and containing hygrophilous grasses, was situated in this part, and was flanked by A. nigrescens and Schotia brachypetala trees.

The size of the study area, which was approximately 650 m x 900 m (0,6 km^2), was limited largely by the method

of observation, which was to park the vehicle on the side of the road and remain in it for most of the day, noting interactions between individuals. In this way, disturbance was minimal after arrival in the area in the early morning, and occurred only when the occasional tourist vehicle passed.

During the first two days, territorial boundaries between six individuals were fairly firmly established, and on the third day the vehicle was parked approximately 250 m north of the first point, enabling the boundaries of a further five animals to be mapped.

The animals were not artificially marked, but differences in the facial markings and in horn sizes and shapes made it possible to recognise individuals through binoculars. The black facial markings in impala vary both in intensity and in extent; in some they are very dark and prominent, and in others completely absent. (Out of curiosity I once subjectively allocated impala, on the basis of their facial markings, into three categories - dark, light and intermediate - at a waterhole count in Mkuzi, and found the proportions to be 96:87:267, or approximately 1:1:3. A geneticist may find this significant).

5.3. Results.

5.3.1. Territoriality.

a) Animals present.

Eleven different males were present in the study area

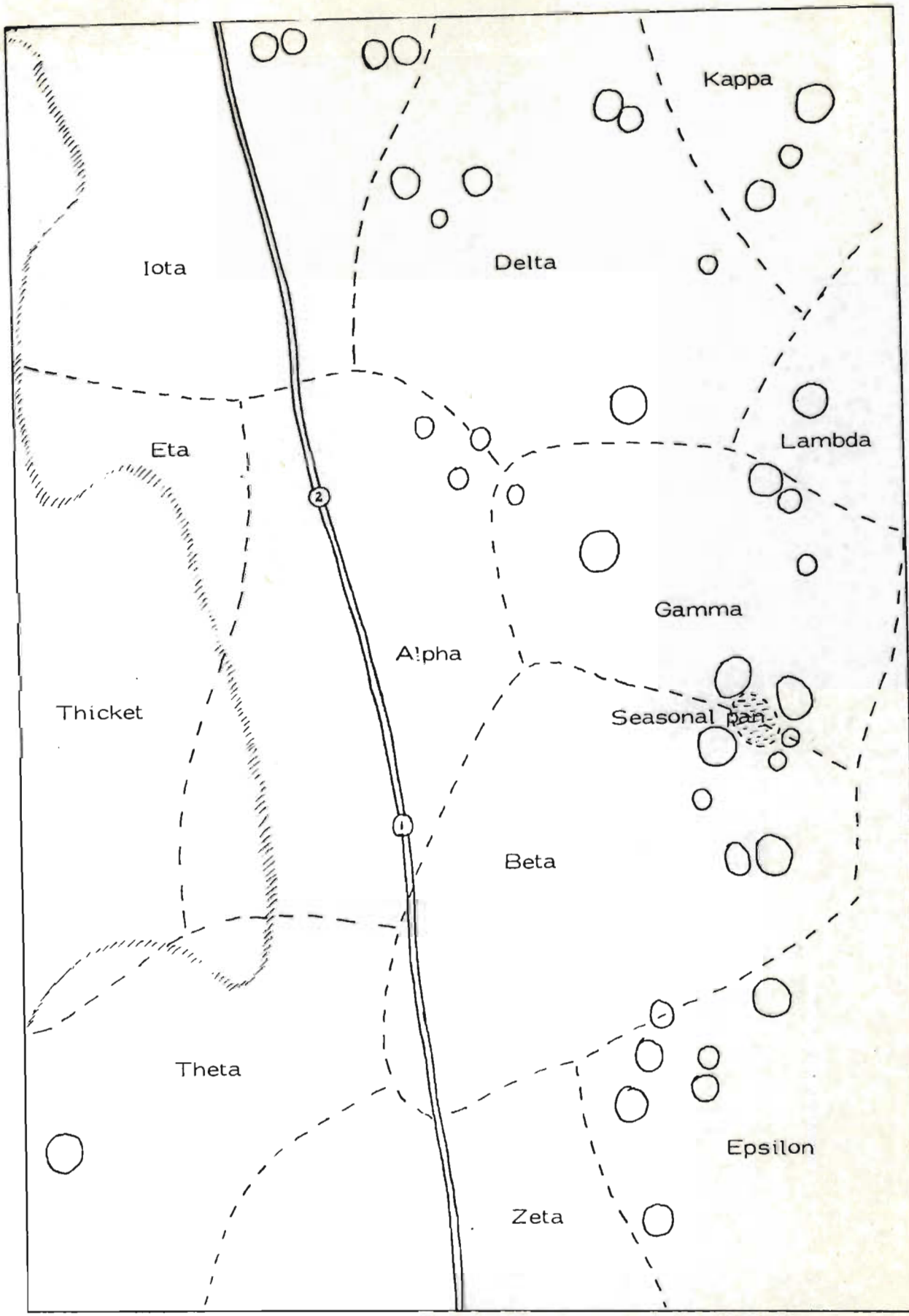

Figure 11. Sketch map of a study area in which observations on on territorial behaviour were intensively carried out showing the approximate territorial boundaries as dotted lines. Circles represent large (>5m) trees.

throughout the period of three days, and remained separate from one another, except for bried interactions, some of which are described. These eleven males were arbitrarily given names corresponding to letters of the Greek alphabet, in the order in which they were first seen, and their characteristics noted for subsequent recognition (see Figure 11). On the third day, a group of four immature males (18 months old) emerged from the thicket in the north-east of the study area and passed through three successive territories before disappearing from view. One group of two adult males and, on a separate occasion, a single adult male, entered the study area on the first day.

Four apparently different female herds consisting of seven females and two juveniles, ten females and six juveniles, four females and three juveniles, and thirteen females and nine juveniles respectively, also entered the study area at various times, and remained for varying periods ranging from about half an hour to nearly four hours.

A number of steenbuck and warthog were apparently resident in the area, while two herds of wildebeest also entered, stayed briefly, and left again.

b) Boundary determination.

The location and movements of all impala seen during the entire period of observation and the points at which interactions took place were plotted as accurately as possible on a sketch map of the study area drawn from an aerial photograph and augmented by ground observations. A different map was used approximately every two hours, depending on the activity taking

place. Activity was recorded on a tape recorder and transcribed later.

At the end of three days, these maps were superimposed on one another, and the limits of activity of the territorial males drawn in as shown in Figure 11. It was necessary to make some extrapolations to complete the various boundaries between the territories of certain individuals but, if it is assumed that the boundaries are reasonably "smooth" and without irregularities, then those shown are quite accurate.

c) Territory sizes.

Only four complete territories fell within the area which was intensively studied, and their respective sizes, calculated with the help of a planimeter to the nearest 100 m^2, were as follows:

Alpha	64 500 m^2.
Beta	72 800 m^2.
Gamma	48 800 m^2.
Delta	78 000 m^2.

The mean size was therefore 66 000 m^2, equivalent to a mean diameter of 290 m.

The territorial boundaries of the remaining seven animals could not be completely determined, for these animals occasionally disappeared beyond the limit of visibility, and were presumed to be still within their territories.

d) Behaviour of territorial males.

The behaviour of the territorial males whilst on their own, when in interaction with one another, in the presence of other impalas, and towards other animals - at all possible times in fact - was noted.

At most times the territorial males were alert and restless. The (edited) Day 1 log of male "Alpha" shows typical patterns of behaviour exhibited by all the males (See Figure 11). Other males were given names corresponding to successive letters of the Greek alphabet, abbreviated in the notes to the initial.

06h45 Arrival. Alpha disturbed, approx. 70 m right of observation point. Ran into thicket.
06h58 Emerged from thicket, followed by Eta, snorting. E stopped, A ran across road behind. Delta alerted, ran toward A, snorting. A attacked D. Vigorous fighting, no damage. Broke off, both roared and retreated, A toward vehicle. Gamma approached A, stopped approx. 80 m from A's line, snorted. A stopped, turned towards G, roared, and ran towards G, roaring. G stood, A stopped approx. 30 m away. G turned, fed. A walked towards vehicle, stopped, defaecated. Alert.
07h12 A approached close to vehicle, watchful. Snorted. Looked at Beta approx. 100 m away (B walking south to north). A watched carefully.
07h28 A walked past to south, approx. 20 m east of vehicle, watchful. Crossed road. Theta appeared from behind thicket, saw A,

alerted. A stopped. T snorted. A ran west of vehicle, parallel to road.

07h40 A feeding, stopped at dungheap, sniffed it, defaecated. Stood, head up.

07h59 A carried on feeding, crossed road, stood under a tree. Looked towards D and G in turn.

08h34 A feeding. Seven females, two juveniles in D's territory. D appeared, roaring. A alerted, walked towards females, stopped and gazed towards them. Head up, snorting periodically. D between A and females attentive to females, uneasy.

08h49 A approached closer, D attacked, A retreated, stopped, turned, roared. D stopped turned to females, ran, roared.

09h03 D chasing females, one broke away, ran toward A, D in pursuit. A attacked D. Vigorous fighting for approx. two minutes. No damage. Rest of females joined first one behind A. A broke off, D roared and retreated. A headed off females, roaring.

09h09 Females crossed road. A attentive to females, grunting quietly. Females feeding, A alert.

09h27 One female ran into thicket. A chased, snorting. Female emerged, A following. Female joined rest, A ran round them, roaring.

09h32 Females moved towards thicket. A tried to head them off, unsuccessful.

09h35 Females, followed by A, disappeared. Much roaring from thicket.

09h57 A emerged, crossed road. B watching. A stopped approx. 20 m left of road, alert, watching B.

10h11 A defaecated on dungheap - same one as before. Remained alert.

10h20 A started feeding, moving northwards, parallel to road.

10h27 A stopped feeding, looked towards Delta/Iota, head up.

10h32 A resumed feeding, moving south-west, crossed road.

10h51 A stopped, lay down, head up. No activity anywhere.

12h41 Gamma snorted. A stood up, alert, watching G.

12h52 A moved farther west, stopped, urinated, moved few more paces to dungheap. Defaecated. Moved into thicket, out of sight. Probably resting.

14h07 A emerged, moved south-east, as if to pass vehicle. Stopped, watching vehicle.

14h10 Roaring from direction of Eta, in thicket. A ran to edge of thicket, snorted three times. Walked into thicket.

14h14 Much roaring. Two males emerged from thicket, one in full pursuit of other, no noise. Ran flat out across road, towards G. D ran roaring towards two males, G ran, roaring, towards D. D took no notice of G, but joined pursuit, stopped, roared. (It was established, once the various boundaries had been located, that Delta had entered Alpha's territory to join the pursuit, but stopped shortly after entering Gamma's territory).

G started chasing the two males, chased D who ran north. G continued after two males. Back one (turned out to be A) stopped, faced G. Clash of horns, A broke off and ran back into his territory, followed by G, roaring. (Other male, adult unknown, continued running east). A and G fought, G gave way. Broke off, both roared. Both stood alert, then walked away from each other.

14h20 A still alert. Watched thicket, walked across road to thicket.

14h24 Eta appeared north of thicket, accompanied by seven females and two juveniles (presumably same group as seen earlier). A approached. E herded females back, away from A. Females ran round, towards Iota, who was also watching.

14h30 E tried to head off female. Iota ran towards him, roaring, threatened, head down. E turned and retreated, roaring. A joined females, I chased, females ran towards south. I and A engaged fight. A retreated, still fighting. I broke off, turned roaring, A stood and watched, roaring. A alert.

14h34 A turned, ran towards female. Sniffed genital region of two of them, adopted proud posture. Females feeding, crossed road, A followed approx. 10 m behind, occasionally stopping and adopting proud posture.

14h58 Females approx. 100 m north of vehicle. B approached, watching, snorted. A did not react, although alert.

15h10 Females approached to within 50 m of B,

who had not moved. A approached females, roaring. Stood between females and B, faced females, proud posture.

15h16 Females grazing towards G, who was also watching, alert. A between females and G. B approached, roaring, fought briefly. B broke off and ran back.

15h18 Two females broke from others, ran past G who followed. A cut off remainder, tried to herd them back. Females ran southwards fast, around A, rejoined others who were being followed and attended by G. A stopped, roared, stood.

15h31 A alert, snorted, facing south. Theta approx. 200 m south-west of vehicle, alerted, snorted. A ran towards T, stopped, snorted. T approached, first running, then walking, snorted three times.

15h55 A and T approx. 20 m apart. Both butting, snorting. Approached each other slowly, turning to lick flanks. A snorted, T threatened, A turned away, stood sideways to T.

16h00 T started feeding, A roared, walked away, close to vehicle.

16h14 A feeding, frequently lifting head. Stopped, watched Eta, who was feeding.

16h20 Vehicle approached from north. A watched, crossed road, ran approx. 100 m to edge of territory, stopped. Stood, alert, watching vehicle.

16h27 G approached slowly, in stages, snorted twice. A walked towards road. G stood, alert, watching.

16h31 A started feeding.

16h40 Roaring display between G and B. Fought vigorously. A ran across road, stood approx. 15 m from G and B, roared. B broke off, ran south, A chased, roaring. A stopped, B stopped approx. 10 m away, turned, roared, chased A flat out. Stopped at A's boundary, roaring. A roared with back to B. Alert.

16h49 A walked to dungheap, defaecated. Rubbed face on twig. Walked north-east towards G who was at other end of territory. Rubbed face again, roared. D roared, walked towards A, who roared back.

16h57 A feeding. Roaring to east, A took no notice.

17h08 Vehicle passed south to north. A looked up, resumed feeding. D and I roared at each other, A alerted, stood still.

17h14 A resumed feeding.

17h30 Observations terminated.

This sequence of events in which Alpha was directly involved, or which affected his behaviour, has been carefully documented in order to indicate patterns of behaviour which were repeated by other males on the first day as well, and by all males on the next two days. These behaviour patterns will be discussed in Chapter 5.4.

The presence of two male groups (the third incursion involved a single male as described above), and of the four female groups, elicited certain aspects of behaviour which are described in some detail here. The two adult males, which appeared briefly at the extreme southern range of vision, passing from west to east,

did not remain long enough for interactions of any note to be recorded. They ran through successive territories, without making any vocalisations, although the territorial males involved showed considerable excitement, mainly after the intruders were passed, with roaring displays being most prominent. These territorial males did not approach closely enough to one another for interactions to take place.

The four immature males likewise created a great deal of excitement. They emerged from the thicket in Alpha's territory early in the afternoon. Alpha was unaware of their presence for a few minutes, as he was resting in the southern part of his territory, with his back towards them. The immature males appeared very nervous, and exhibited a certain amount of aggression towards one another, with butting/nodding motions of their heads. Gamma, who had also been resting, snorted loudly and was then seen to be standing, gazing intently at the young males. This snort apparently alerted Alpha, who rose and rushed towards Gamma, before noticing the presence of the intruders. He reacted immediately by turning on them in a headlong rush. The immature males immediately split up, two returning into the thicket, and the other two crossing the road and running flat out towards Gamma and Delta, who had by now also approached. Alpha stopped near the middle of his territory, just off the road, and roared, facing the second pair of males. They meanwhile ran between Gamma and Delta and kept going towards Lambda. Gamma and Delta did not chase them, but started a vigorous fight near the point where the territories of Alpha, Gamma and Delta joined. Alpha approached to within 20 m of Gamma and Delta and went through

a prolonged roaring display without becoming directly involved in the fight. No further sign was seen of the two immature males which had returned to the thicket from whence they had earlier emerged.

The presence of the various female groups of which only one has been described (as it was presumed that the two appearances involved the same group), elicited a good deal of herding behaviour on the part of most of the territorial males under observation. The largest group, of 13 females and nine juveniles, remained in the study area for nearly four hours. Most of this time was spent in Gamma's territory, much of it at comparative ease, feeding and resting. The group entered the study area from the south-west at midday, passing through Theta's and Beta's territories. Neither male succeeded in holding them for any length of time, despite attempts at heading them off and herding them by circling. In doing this, both behaved in a similar fashion - making butting movements with the head held low. A territorial encounter, with vigorous fighting, between Theta and Beta, provided an opportunity for the females to cross unmolested into Beta's territory. Beta did not succeed in keeping the females for more than a few minutes, for his efforts at herding resulted in the herd running into Gamma's territory, leaving Beta roaring, while Gamma controlled them.

The females then settled down, and rested in the shade of the large trees close to the dry pan, while Gamma stood close by. No other male made any attempt to interfere until, at about 15h45, the females started moving. Gamma herded them towards the centre of his territory, apparently sniffing each

female in turn. When he attempted to copulate with one, the whole herd started running north-eastwards, and Gamma chased them, roaring at length, and apparently concentrating aggression on two juveniles which were running to one side. He followed the herd into Lambda's territory and disappeared from view, to return a minute or two later, roaring again.

e) Marking.

Schenkel (1966a, 1966b) and Leuthold (1970) did not recognise the role of scent marking in impala, although they did report "face-rubbing" in certain situations. The reason for the failure to associate face-rubbing with scent marking is that impala have no preorbital glands. However, Jarman and Jarman (1974) state that there is a glandular area of the skin on the forehead, which is rubbed against bushes to leave a secretion.

In Mkuzi, the action of face-rubbing was seen on several occasions in territorial situations, both when a male was on his own, and when accompanied by females. It was not seen in non-territorial animals.

When scent marking in this way, a male sniffs a twig before rubbing his face (anterior to the eyes), not his forehead, on a portion of the twig. In appearance the secretion is dark brown; it is sticky in texture, but no smell could be detected. The quantity deposited is about half the size of a drop of water, and is not always in one globule.

Dung heaps are invariably found in territories although,

as with scent-marking, they are not necessarily along the boundaries, but apparently randomly distributed within the territory. An examination of the territory of Alpha revealed seven such dung heaps, one of which was seen to be used on more than one occasion immediately after the territory-holder had risen from resting.

No association between urination and territoriality could be detected, as it seemed to be performed at random.

Other forms of territorial display which could be described as "marking" are described in the following section.

f) Display.

Territorial advertising is a necessary activity for the reinforcement of the dominant status of the individual. It has not been documented in impala, although Jarman and Jarman (1974) discuss the subject briefly. It corresponds to the phase which is described by Walther (1972) as "the peak of territoriality", when a male has established his dominance. Various forms of territorial display have been described for other ungulates, e.g. wildebeest (Estes 1968).

In the intensively studied group of territorial impala males in Mkuzi various displays other than marking were recognised in the context of territorial advertising, although I do not claim to have recognised all of those that might occur.

(i) Vocal displays. There are numerous vocalisations emitted by impala most of which do not appear to have been described previously. However, the two most used in territorial

behaviour are the alarm snort (which is used in other situations as well) and the roaring display, both described by Schenkel (1966a, 1966b). The alarm snort may be used when other individuals – not necessarily territorial competitors – enter a territory, and the occupier first spots them. It may then be followed by chasing in the case of male intruders, or by herding in the case of females. The snort is not always a prelude to chasing or herding.

The roaring display appears to be a vocalisation used exclusively in male aggressive and territorial behaviour. In Mkuzi it may be heard as early as the latter part of January, when adult males start chasing one another at a very low intensity. The frequency and intensity of the roaring display increase over the next few months to a peak in April and May, when the sound bcomes a feature of Mkuzi. Although the impala is mainly a diurnal species (M.V. Jarman and Jarman 1973) intense activity takes place at night during the rut.

Males using the roaring display mainly as means of ritualised aggression towards other males, but it is also used by males in presence of females, directed at either nearby males or occasionally apparently at the females themselves. It is most commonly heard in situations of considerable excitement, when it may serve as a warning as well as a display of dominance. Leuthold (1970) detailed the occasions on which 22 roaring displays were observed, from which it is clear that assertion of dominance is largely involved. Jarman (1974) points out that roaring is associated with aggressive territorial activity.

(ii) Optical displays. Clearly the mere presence of a

male on a territory is usually a demonstration of his dominance, and it is advantageous to be able to advertise this presence with the minimum of effort. Estes (1968) described a form of display in wildebeest, which he called "static-optic advertising". It has also been described for black wildebeest Connochaetes gnou (von Richter 1972) for red hartebeest (Kok 1975) and for several other species. von Richter (1972) also described "dynamic-optic displays".

The static displays seem to be particularly well developed in alcelaphine entelopes but are not peculiar to this group. Leuthold (1966) alluded to the habit in Uganda kob Kobus kob, which has a similar territorial system to that observed in impala in Mkuzi.

Impala in Mkuzi do stand in their territories, and this is taken as a form of territorial display, for the reason that they spend more time standing than lying down. At other times of the year, males frequently lie down to rest, and females do so at all times of the year.

g. Threat behaviour. Schenkel (1966a) described various conflict situations between impala males in considerable detail. All these situations were observed in Mkuzi, although the relative status of the participants could not always be determined. Threat behaviour is a common thread between all the interactions described.

The basic nature of threat behaviour between males consists of a lowering of the horns. The degree of lowering varies, depending on the situation, between a very slight

bobbing of the head, which is often sufficient to scare off a rival, to a position in which the head is held very low, with the horns pointed forward and almost touching the ground. The extreme instance is a forward rush towards the rival, resulting either in the inferior male taking flight, to be followed by the dominant one, or in a fight, which may be a very brief clash of horns or a prolonged combat.

When herding one or more females, a male may adopt similar threat postures towards the females. Their reaction is invariably to move away, which is obviously the motive of the threat. At times the threat may result in one or more females running off. This is thought to be the result of a too intense threat for the particular situation, possibly when directed at a very submissive female.

h. Fighting. Schenkel (1966a) described situations in which the end result was a fight between males. Although his observations are not interpreted in the context of territoriality, fighting in such a situation does occur.

Fighting or play-fighting takes place among males, females, and juveniles, but was never observed between the sexes. Juveniles often play-fight by pushing against each other with their heads; these fights are never vigorous, but take the form of very gentle nudging. With increasing age, males play-fight more frequently than females, and again this lacks any real aggression. Adult females occasionally do this too, also without manifesting any aggression.

Fights between adult males vary in the intensity of

aggression, with the relative status of the combatants. Most fighting takes place between territorial males, so that they are of high intensity, although not very prolonged. The longest fight seen in Mkuzi lasted less than a minute.

Territorial fights seldom take the form of a brief clashing of horns, but involve vigorous pushing with the horns interlocked. The fight may move to and fro across a territorial boundary, as first one and then the other combatant yields, although the fight does not necessarily follow a linear form: it may be circular, with the combatants circling at times. Movements are very rapid and it is not always possible to follow the individuals closely. The direction of yield is not always in the direction of the respective territories. Nevertheless, when the fight is broken off it always occurs when an animal is backing on to its own territory. In those encounters which are linear an animal always fights to defend his territory, with his back to it.

The combatants are silent whilst fighting, but on separating, one or both generally indulge in a prolonged roaring display, and seldom resume their fight. Damage to one or other of the bombatants does not often occur, although adult males with one broken horn are frequently seen, and a number of mortalities attributable to horn wounds are reported annually - nearly always in the period April/ May.

It was not possible to confirm Schenkel's (1966a) observation that fighting is a result of aggressiveness overcoming the inhibition to fight, either as a result of

momentary distraction creating an imbalance of tension, or as a result of the inhibition being overcome simultaneously in both partners.

5.3.2. Herding.

Territorial males direct a good deal of energy towards herding females within their territories, and in trying to keep them there. As soon as a group of females is inside a territory and the male is satisfied that there is no further threat from the occupier of the territory first vacated, he busies himself keeping the females away from his territorial boundaries, and then preventing them from leaving.

In this, no male is absolutely successful, as there is no way in which he can keep females confined, for the two main reasons that a territory does not contain all the resources needed to support this group, and that the territory-holder is being continually distracted by the attentions of neighbours. Only when a female herd chooses to rest within a territory, does it stay for any appreciable length of time.

The actions of herding consist mainly of simply directing the females in a desired direction, if they are on the move. To do this a male emits a very low-intensity roaring, in which the grunts ("coarse bleating sounds" of Schenkel 1966a) do not follow the snorts as in the typical roaring display. Females usually react by turning in the required direction, but very often one will break away and make determinedly towards some other territory, whereupon others follow. The male may either give chase, sometimes succeeding in turning the leading

female, but more often simply spurring the other females to move faster and thus losing them altogether to a neighbour. He may also succeed in herding off only a portion of a herd of females, losing the rest, and thus splitting a female herd.

Evidence for female herds having been split up is seen in the existence of confused groups of females apparently looking for others. In this way too, juveniles may become separated from their mothers.

When herding a group of females containing juveniles and sometimes yearling males, a territorial male may direct aggression towards one of the latter. This causes confusion amongst the remainder of the herd and sets off a fight reaction.

Outside the period of peak territoriality - the rutting season - many of the breeding herds are accompanied by one or more adult males, corresponding to the "Harem" situation suggested by Schenkel (1966a). However, there is no breeding activity except for a brief "secondary rut" in September, which has been described by Anderson (1975). The presence of these males with the breeding herds has no significance and is probably simply a manifestation of the gregarious instinct of the species. Incipient herding behaviour may occur, but the females do not react. The association is more permanent than it is during the rut, in the territorial situation, and the accompanying males may apparently remain with the breeding herds for considerable periods.

5.3.3. Chasing.

Chasing by a territorial male is elecited by the presence

of any bachelor herd or by the undue proximity of another territorial male. The reaction starts with an alarm snort, which is followed by an approach with a slow gallop. If the intruders flee, the territorial male may break into a full speed chase accompanied by roaring. If they do not he threatens, and resorts to bodily contact and fighting only as a last resort.

Schenkel (1966a), Leuthold (1970), and Jarman and Jarman (1974) all reported that bachelor males are tolerated in territories, as long as they keep away from females, but this was not the case in Mkuzi, where all bachelors were very quickly evicted from territories.

Chasing is not characteristic only of the period of territoriality, for it takes place throughout the year in various degrees of intensity. Outside the rutting season it is of a very low intensity, and only very occasionally is a serious chase seen.

In late January, as has been described under vocal displays, the incidence of roaring starts to increase. These roaring displays are frequently accompanied by chasing, which occurs within bachelor groups of adult males. The main effect of this activity is to increase the interindividual distance between adult males, leading up to a peak in territoriality. This will be discussed in the next chapter.

5.3.4. Courting.

Schenkel (1966a, 1966b) described several behaviour

patterns associated with courting displays, as follows:

a. Nose forward posture with empty licking.
b. Pawing and licking gesture.
c. Lateral display.
d. Rising on hindlegs.
e. Grunting display.
f. Bleating display.

Only the first mentioned of these was observed in Mkuzi. It occurs frequently when a territorial male is attending a group of females, and not only during the rut: adult males accompanying breeding herds also do it from time to time, so that the significance is not clear. It may not have any association with courting at all.

The pawing/licking and lateral displays may have been overlooked because of the comparatively few times that females get an opportunity to rest in the company of territorial males.

5.3.5. Mating.

The point at which the male's behaviour in herding females becomes courtship is not clear cut, although Schenkel (1966a) puts it at the time that chasing is directed at one particular female, and is not accompanied by roaring.

The situation in Mkuzi differs from that described by Schenkel in that there is a rutting season, when nearly all the females have to be mated in a comparatively short time - about two to three weeks. In East Africa, on the other hand, females may come into oestrous at any time of the year.

Furthermore, in East Africa, a herd of females spends more time with a territorial male, who therefore is able to devote more time to courtship.

In Mkuzi therefore, courtship is abbreviated in comparison to the same process in East Africa. The various phases described by Schenkel (1966a) are not readily apparent, and the territorial male may try to mount a female at any time he has the opportunity. Copulation is not always preceded by a chase, but is only successful when the female is ready to accept the male. Nevertheless, chasing females without roaring is a pattern of behaviour.

Copulation was observed only on two occasions in Mkuzi, in each case by a territorial male. It is a very rapid action, and the posture noted agrees with that described by Schenkel (1966a): the male does not grip, or apparently even touch, the female's flanks. Immediately after copulation, the male goes into a roaring display.

Several attempts at copulation were noted, although in each case the male came nowhere near the female, which ran away. This may correspond to Schenkel's "third premating phase", but I prefer to look upon it simply as an unsuccessful attempt at mounting due to lack of receptiveness of the female.

5.3.6. Parturition.

Jarman (1976) observed and described in detail the parturient behaviour of impala in East Africa. Birth was not

observed in the Mkuzi study, although associated behaviour was noted on several occasions, and is described here only as circumstantial evidence of parturition.

The very short breeding season of impala in Mkuzi - two to three weeks - means that a number of females in a herd may approach parturition at the same time. Small groups of two to four females (and sometimes just one), which are obviously still very pregnant, detach themselves from the herds and may be seen in secluded spots, usually in dense bush. They are highly nervous and their flight distance is a good deal greater than normal.

Birth presumably takes place in dense cover, although there is no direct evidence from this study of the time of day at which most births take place. Indirect evidence is in the form only of two placentae which were seen on the same morning, very early, and not in the same area. M.V. Jarman and Jarman (1973) and Jarman (1976) report that East African impala have a preference for giving birth in the middle of the day, although due notice is given that the absence of nocturnal observations does not necessarily imply that birth does not take place then as well.

Jarman (1976) also states that the female consumes the placenta shortly after birth. The two records of unconsumed placentae, both seen on open ground, are not conclusive evidence of a different pattern in Mkuzi. Because they were in the open may mean that the females were disturbed before eating them.

Very young, still unstable, juveniles were seen on four occasions all in the early mornings, and all close to dense cover. On one occasion there were two together, with their mothers. On all occasions these new-born animals were some distance from the nearest herd.

Jarman and Jarman (1974) state that young may lie out for several days after birth. In Mkuzi non-pregnant females in small groups of two or three animals, were seen without young on several occasions, suggesting that the juveniles were either hidden or had been lost. Erasmus (1964) reported having culled females which were not accompanied by juveniles, but which were lactating heavily. Whether lying out is a charateristic feature of impala behaviour is not yet known.

Groups of females were also seen in the company of juveniles, and the older the juveniles, the larger these groups became. This suggests that the gregarious instinct returns when the young are old enough to keep up with the adults. In this way the large breeding herds characteristic of the summer season were formed. This will be dealt with in Chapter 6.

The strictly seasonal nature of breeding of impala in Mkuzi also means that there is none of the sort of interference of a parturient female by a territorial male which was mentioned by Jarman (1974). There may be some interference caused by the natural inquisitiveness of other impala, but even this is minimised by virtue of the fact that most of the other females are in the same condition at the same time.

5.3.7. Mother/young bonds.

Jarman (1976) discussed the formation of mother/young bonds, saying that the following instinct of the young is undirected at first. This is confirmed in the Mkuzi study, for the new-born young appear quite uncoordinated, and the females are forced to stay close in order to remain with them. This lack of a firm bond on the part of the juveniles remains a feature even after the large herds have been formed, and it is never possible, except when they are nursing, for young definitely to be identified with their respective mothers. The brief period of concealment of the young and of isolation of the mother probably familiarises the young with its mother even if a firm and longlasting bond is not forged.

Jarman (1974) also stated that kinship is not responsible for an animal's association with other females, although Schenkel (1966a) postulated that there may be a lasting affinity between mother and daughter. Anderson (1972) suggested that the mother/young bond persisted even up to the next season of births, because he observed a pregnant female accompanied only by a yearling male or female, presumably her offspring of the previous season.

An observation in Mkuzi (Behr 1968) conflicts with a statement by Jarman (1974) that impala do not generally cooperate in aggression against predators. In this instance two females were seen attacking a jackal which had already bitten a lamb; they then chased it off. This suggests that there is a form of cooperation, although it is probably not well developed.

5.3.8. Creches.

Fraser (1968), Anderson (1972), and Jarman and Jarman (1974) all refer to what are variously called "nurseries", "nursery herds", and "creches". The impala nurseries of Fraser (1968) are probably the creches of Anderson (1972) and Jarman and Jarman (1974), whilst the nursery herds of the latter two authors are the breeding herds which are described in the next chapter. Schenkel (1966a) observed the formation of sub-groups, which he called "nursery groups" within the breeding herds; these are simply associations of females with juveniles of the same age.

In the Mkuzi study the actual formation of creches was observed on two occasions, whilst their presence was noted frequently, both in Mkuzi and elsewhere in Zululand. Their occurrence is limited to within a few weeks after birth of the young, until the juveniles come to rely less on nursing and indulge more in feeding on their own.

One particular observation on creche formation clearly shows the significance of this group. It took place at one of the waterholes on 19 December 1970.

> A group of 23 adult and immature females, two immature males, and 9 juveniles (approx. 3 weeks old) arrived at the waterhole at 10h25. The males and two of the females went straight to the water and drank, while the remaining females and juveniles moved slowly about, the females feeding and the juveniles simply

following. The latter occasionally interacted by play-fighting or skipping nimbly about.

One of the drinking females was accompanied by a juvenile which approached the water and sniffed it, but did not drink. All those which had been drinking moved off and started feeding in the vicinity, whilst the rest of the females drank in succession over a period of about 15 minutes. None of the juveniles drank water.

Starting with the juvenile which was with the female that first drank, all the juveniles started suckling shortly after their mothers left the water. While they were nursing the females stood still, although they did occasionally sniff the anal region of their respective young. In each case, the mother instigated the cessation of nursing after about two minutes, by walking away - in one case by running off for a short distance.

The females all then resumed their own feeding while the juveniles played among themselves for about five minutes. This activity showed a marked decline in intensity, and one by one they lay down until all were resting in an area about 3 m square, around a small bush clump. The remainder of the herd went on feeding until they were out of view, two of the females lagging behind for a while until they also disappeared. All were out of sight by 11h15.

I remained watching the group of juveniles.

At 11h35 two adult males approached the waterhole from the other side. They were feeding and showed no sign of having noticed the resting juveniles. They did not drink, but walked past the waterhole for a short distance before standing under a tree and ruminating.

No other impala came near the waterhole, but three groups of warthog came to drink. One group showed interest in the impala but did not disturb them and moved off.

At 12h22 a single adult female was seen approaching from the direction in which the herd had disappeared, at a distance of about 50 m. I did not hear anything, but she was gazing intently towards the juveniles, alternately walking slowly and standing still. One juvenile lifted its head and uttered a bleat, whereupon all the others awoke, stood up and moved in the direction of the female at a run, all bleating. The female ran to meet them, sniffed them as they ran past, then turned and followed. No other female was seen, but it was assumed that the remainder of the herd was out of sight to me, but either visible to, or within hearing of the juveniles.

One other instance of creche formation was seen under different circumstances the next day. I had stopped my vehicle to watch a breeding herd, also at about midday, in an area of dense bush clumps with open, short grass between the clumps. The pattern was much the same, with six juveniles all starting

to suckle within a few minutes of one another, whereafter they lay down in some shade against a bush clump while the females resumed feeding, moving off slowly. On this occasion one female remained behind, although I did not stay to watch subsequent events.

The formation of creches is a very temporary phenomenon, and I did not see any such groups after the first week in February. From the detailed observations made on the two occasions described, creches are clearly simply a result of the normal reaction of young animals after they have fed, namely to sleep. The mother/young bond is temporarily broken in these periods but is quickly restored, at least until the juveniles are fully weaned, when they keep up with the herd and the gregarious instinct becomes dominant.

While in creches the very young animals may be more vulnerable to predation than at other times, although no instances of predation on creche groups have been recorded.

5.4. Discussion.

Territorial behaviour is an established feature of the behaviour of impala both in East Africa (Leuthold 1970, Jarman and Jarman 1974, and Leuthold 1977) and in southern Africa (Dasmann and Mossman 1962, Mason 1976, and this study). Schenkel (1966a, 1966b) described features of impala behaviour which could have been interpreted as territoriality, but he did not recognise them as such. Later (Schenkel, in litt.) reiterated his belief that impala are not territorial in the sense that they

defend a piece of ground. He did go on to say however that a male dominates a female herd, in the immediate vicinity of which he is intolerant of other males. This intolerance, he believed, is ".... focussed on the female herd, and not on his home range.....".

The actual definition of territoriality will be discussed in Chapter 6 for it is important in the social organisation of the species. For the present, only those aspects of territorial behaviour not directly related to social organisation will be discussed.

Dasmann and Mossman (1962a) recorded the presence of dung piles and noted that they are associated with territorial behaviour. Leuthold (1970) also found dung heaps, but attached no significance to them in the territorial context. Jarman and Jarman (1974) went further to say that these heaps might also be used by females and bachelor males. No author has at any stage claimed that the dung heaps are used to delineate a territory, although they may more easily elicit some reaction in the individual during the period of territoriality. In the present study dung heaps were more evident during the period March to May, corresponding with the rut, but were not associated with the boundaries of the territories. It is thus concluded that their presence is a manifestation of territorial behaviour in impala whose significance is not clear.

The observation that impala territorial males frequently defaecated on one of the heaps on rising from resting may indicate that their situation is associated with favoured

resting places which could have some static-optic significance.

Estes (1974) placed the impala at an "intermediate" level of social organisation, and this may be an explanation for the apparent randomness in the placing of dung heaps by territorial males: its behaviour may not have evolved far enough for territorial marking by defaecation to be properly established. A similar situation was found by Owen-Smith (1975) in the white rhinoceros Ceratotherium simum, in which dung heaps were randomly situated in territories and were used by all categories of animals. Only territorial males indulged in scraping after defaecating, indicating that the dung heaps may have had an incipient territorial function.

Static-optic advertising is well-developed in some ungulates (Estes 1968, von Richter 1972), particularly in the species with the most advanced level of social organisation (Estes 1974). In impala it is not as prominent a feature of territorial behaviour, but is nevertheless important in territorial advertising. Observations on this form of behaviour in Mkuzi indicated that it was an alert posture, and this phase may well have evolved into the more ritualised static-optic advertising in other species, particularly those adapted to an open plains existence.

Another form of territorial marking which was observed was scent-marking, in which the glandular area of the face (Jarman and Jarman 1974) was rubbed on twigs by territorial males. This behaviour was never seen in any other social category, including bachelor males, and the glandular nature of the face may be only a seasonal feature associated with

territoriality.

The significance of a roaring display was described by Jarman and Jarman (1974) as an expression of some aspects of the male's territorial status. This may be the case in East Africa where year-round territoriality is the norm, but in Mkuzi the roaring display is not confined strictly to the territorial situation. Its occurrence as early as January, five months prior to the peak of the rut, indicates that is is more an expression of aggression. At this time some males had entered the pre-territorial phase, when aggression within a bachelor herd is a prelude to the establishment of territories. With their establishment, roaring is used only as a display of aggression to reinforce territorial advertising.

CHAPTER 6

SOCIAL ORGANISATION

6.1. Introduction.

The social organisation of a population is determined by the interaction of the various patterns of individual and social behaviour described in the previous chapter, and influenced by conditions of the environment and habitat. It involves all the individuals in a population.

The impala is essentially a gregarious species, a fact recognised by everyone who has worked on it, and all aspects of its social organisation are influenced by this habit.

6.2. Herd types.

6.2.1. Classification.

Schenkel (1966a) recognised only two main herd types, namely female or breeding herds, and male or bachelor herds. Later, Leuthold (1970) described five "social groupings": male herds, single adult males, female herds with one adult male, female herds without an adult male, and mixed groups. Anderson (1972) also distinguished five social groupings: lamb herds, female herds, yearling herds, male herds, and lone males. To add to this plethora of terms, Fairall (1972) mentioned female herds, male herds, and breeding herds.

Jarman (1970) was the first to recognise the existence of the three "social groupings" which are now accepted as being normal in impala. These she described as:

1. Lone, adult males,
2. Male herds, of adult and juvenile males, and
3. Breeding herds, of females of all ages and juveniles.

Later in a discussion on gregarious ungulates in general, Estes (1974) recognised three social classes as being universal to all, namely:

1. Territorial males,
2. Bachelor herds, and
3. Female and juvenile (= breeding) herds.

Although impala are gregarious, the herds tend to be unstable in size and composition (Leuthold 1977).

At this point it is necessary to make some distinction between the various terms used to describe the types of group viz. herd types, social groupings, social classes, and social categories. These terms, used by different authors, all refer to distinct variations in the social structure, and it is proposed that the term "social groupings" be used to describe the complete range of combinations of sex and age classes that may be encountered in a population, and "herd types" be used to describe the three basic social units, listed by Estes (1974) and by Jarman and Jarman (1974), and accepted in this study.

6.2.2. Frequency of occurrence of herd types.

A total of 17 different combinations of sex and age classes (social groupings) was recorded in Mkuzi. Some of these were abnormal groupings, created by some means or other; for instance, juveniles on their own or with adult males were not normal. These abnormalities made up only 2,1% of all groups seen.

The various combinations were assigned to one of the three basic herd types, and this analysis is shown in Table 15. Despite the seasonal nature of territoriality, all records of adult males which were not in the company of any other male, and separated from them by a distance of about 25 m or more, were treated as "territorial males". Thus the classification of Estes (1974), which mentions solitary adult males as opposed to territorial males, is preferred to that of Jarman and Jarman (1974) for the purpose of this analysis. Breeding herds may be accompanied by one or more adult males throughout the year, although for much of the time they were not territorial. In the analysis, when one adult male was present, he was considered as "territorial".

The incidence of various herd types is shown graphically in Figure 12.

6.2.3. Territorial males.

In 1971, sampling was carried out weekly during April and May to determine more precisely the peak in territorial

Table 15. The occurrence of the three basic herd types of impala in Mkuzi, expressed as percentages of all herds seen, for each month of the year. (Pooled data for 1970 and 1971 samples).

Month	Territorial male	Bachelor herd	Breeding herd
January	16,2	30,0	53,9
February	20,4	32,8	46,8
March	26,4	26,4	42,2
April	26,5	25,2	48,2
May	40,5	16,6	42,9
June	29,1	21,1	49,8
July	17,6	27,3	55,1
August	29,2	30,3	40,4
September	23,3	23,3	53,4
October	21,8	24,3	53,9
November	19,5	25,4	55,1
December	13,4	27,5	59,2
Mean	23,4	25,2	51,3

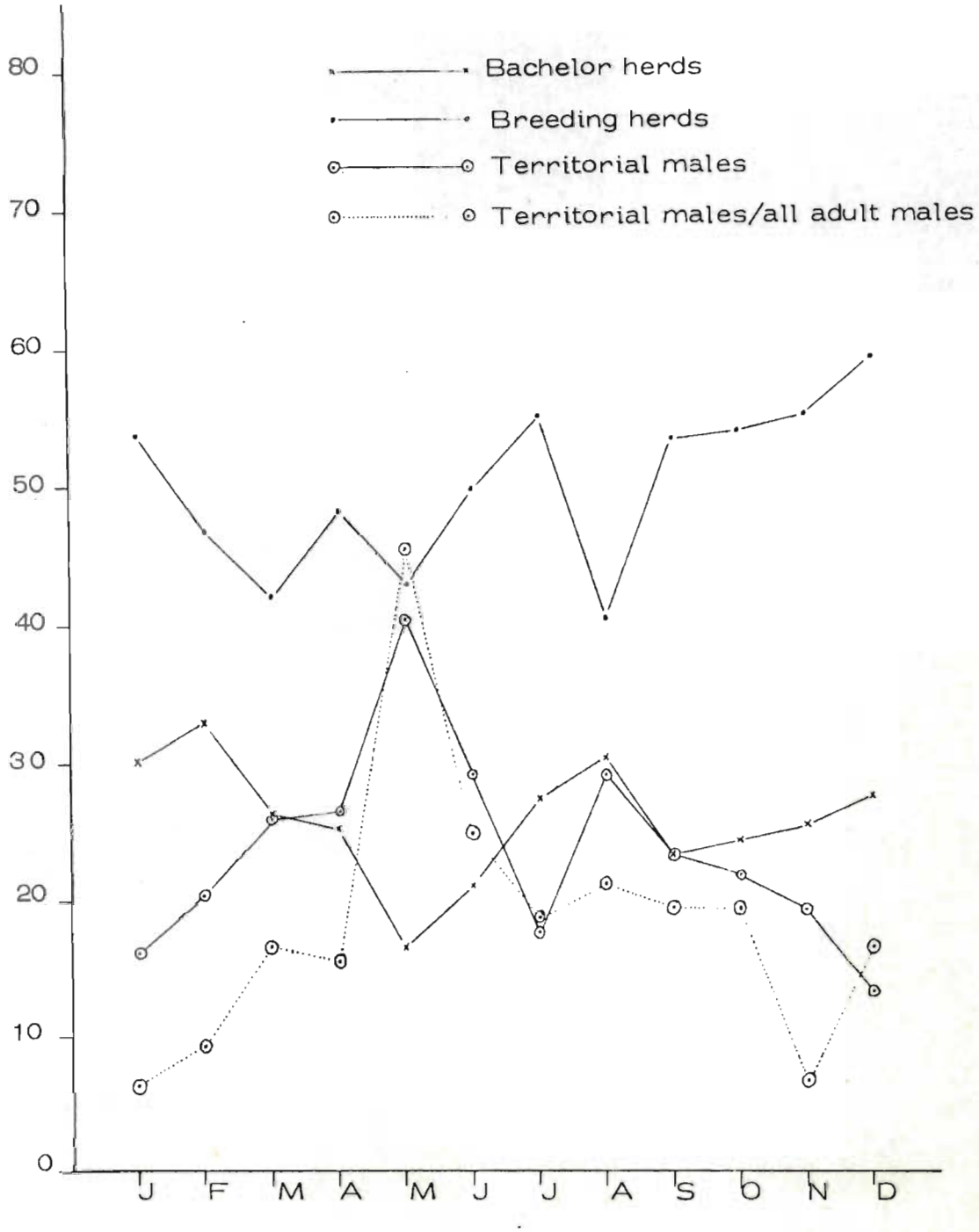

Figure 12. Percentage occurrence of the three herd types of impala in Mkuzi through the year. (Pooled data for 1970 and 1971 samples).

behaviour as reflected in the incidence of lone adult males. As much as possible of the reserve was covered on one day each week at this time. All animals seen were recorded as to sex and social status, and the proportions of solitary adult males are shown in Figure 13 as a percentage of all adult males seen.

The largest proportion of territorial males was recorded in the third week of May, when they accounted for 49,1% of all adult males - 156 of a total of 318 seen in one day. The means for April and May in this specific sample were 24,4% and 41,2% respectively (compared with 26,5% and 40,5% in the main sampling carried out during routine censussing).

Leuthold (1970) presented some statistics which may be directly compared with some of those reported here. For instance, over a period of nine months in Nairobi National Park, the incidence of solitary adult males recorded was 21,7% of all groups observed. This is comparable with the year round mean of 23,4% in Mkuzi Game Reserve. Similarly, the occurrence of lone adult males expressed as a proportion of all adult male groups was 36,6% in Kenya, whilst the highest such proportion in Mkuzi, which was observed during the peak in the rut in May, was nearly double this figure, i.e. 70,9%; the year-round mean in Mkuzi was 48,1% and the lowest proportion was 31,8% in January. On the other hand again, the proportion of breeding herds accompanied by a single adult male was 31,7% in Kenya, which was very close to the 30,3% at the peak of the rut in April/May in Mkuzi. The mean figure for the whole year in this study was 44,5%

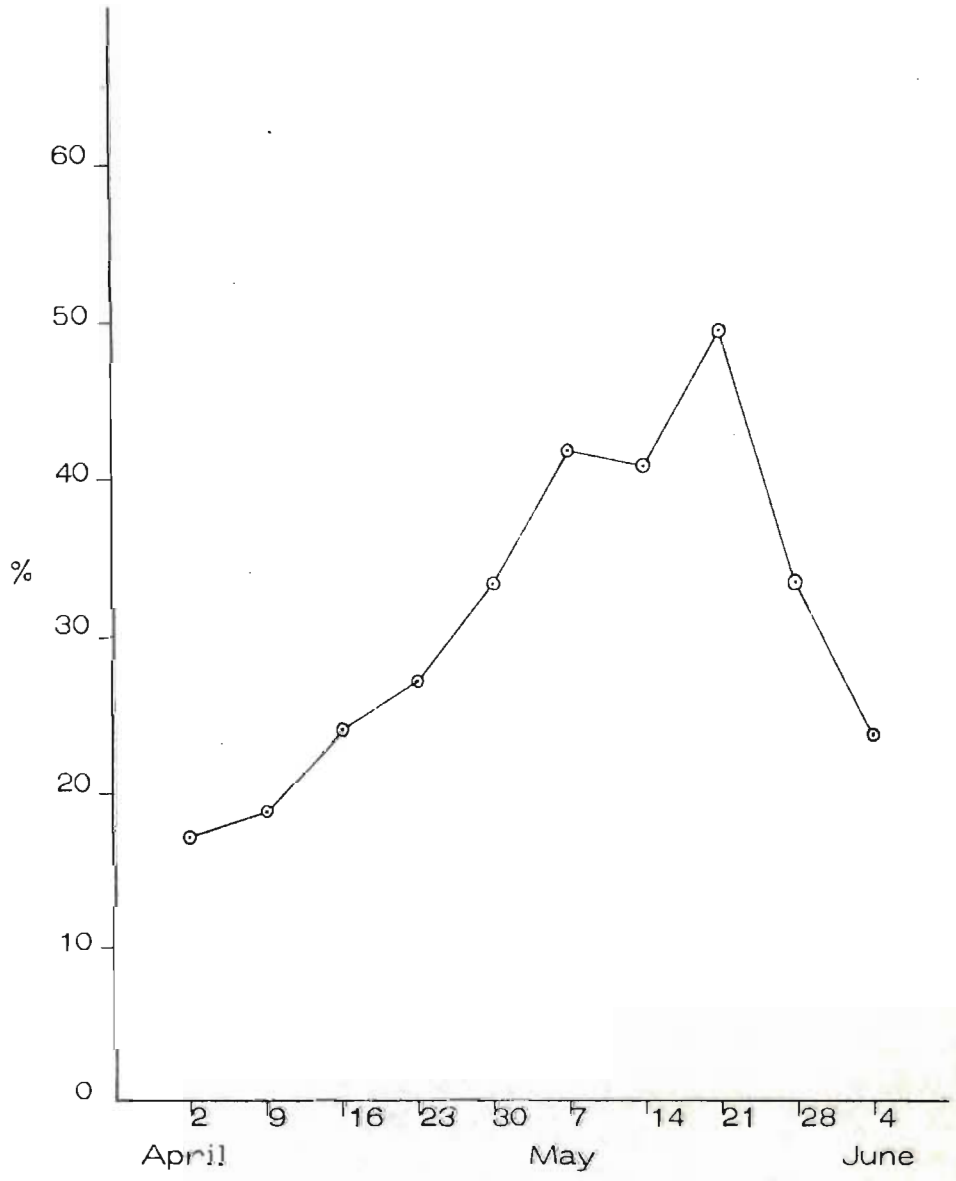

Figure 13. Proportions of territorial males expressed as percentages of all adult males, from samples taken at weekly intervals before, during and after the peak of the rut.

These figures suggest that, despite a higher proportion of adult males in Mkuzi taking part in the rut - as evidenced by territoriality - no more breeding herds were accompanied by adult males during the rut in Mkuzi than was the case year-round in Kenya, where the breeding season is not as well-defined as it is in Mkuzi.

The development of territoriality is a seasonal occurrence, and the incidence of solitary males, shown in Figure 12 demonstrates a slow increase in the proportion between January and May, followed by a rapid decline to July, with a second peak in August/September. This second peak is not as marked as the one corresponding to the main rut, yet a surprisingly large proportion of males (19,5% of all adult males) is territorial. The figure for May is 45,5%.

The occurrence of this secondary peak of territorial activity has been noted by Anderson (1975), whilst Fairall (1972) found that female physiological activity in the Kruger National Park population showed an inexplicable peak in September, in addition to the main one in May. No attempt has been made to account for this secondary peak, although Vincent (1972) reported the presence of a small number of very young lambs in Mkuzi in April, suggesting that there is indeed some sexual activity in late September. The effect of this small number of "out-of-season" births on the overall population in Mkuzi must be minimal. Of nearly 800 juveniles recorded in the routine counts in April and May only seven were clearly much younger than the rest; five were recorded in 1970 and two in 1971.

In so far as male activity is concerned, Fairall (1971) noted an increase in testicular activity in September, whilst Skinner (1971a and b) found a decline in activity from May to a minimum in September. Fairall (1971) also reported an increase in testis mass at this time, while Vincent (1972) found the same in August, but only in younger males, in the first two tooth wear classes described. The incidence of territoriality at this time is a manifestation of this increased activity.

In September 1972 (Densham, pers. comm.), a late capture of surplus impala took place. Males were seen to become very possessive of females in the general excitement resulting from the capture technique described by Densham (1974). They also showed considerable aggression when they were enclosed. This behaviour may be explained by gonadal activity giving rise to territoriality during this "false rut".

For the remainder of the year, various proportions of solitary males were recorded, but these animals exhibited no territorial behaviour of the form described in the previous chapter. Even in September the territorial behaviour was of a very low intensity. Between June and January most of the otherwise solitary males (between 60% and 80%) were seen in the company of breeding herds, thus exhibiting the very basic instinct of greppariousness which is characteristic of impala. These associations were very loose, and the males, often two or more to a herd, made no attempt to herd the females. It is this stage in the solitary male cycle that has given rise to the impression frequently

quoted (e.g. Stevenson-Hamilton 1947) that impala males have "harems".

A harem may be explained as a breeding herd permanently held by a dominant male, and may also be the term given to such a herd when accompanied by a territorial male in the rutting season characteristic of southern populations. In fact Estes (1967) states that true harems are found only amongst the equids (see Klingel 1969, 1972).

In East Africa impala territories are larger - 0,2 - 0,9 km^2 (Leuthold 1970) compared with a maximum of 0,08 km^2 recorded in Mkuzi - so that females are apt to remain for longer in individual territories. It was for this reason that Schenkel (1966a, 1966b) concluded that "there is no territorial intolerance", and that, "The relationship between the sexes is characterised by the constant effort of the strongest males to possess and tend a female herd". In fact a harem is characterised by the permanence of its composition and of the male which dominates it. This situation is not usually found in impala (Jarman, pers. comm.), although one approaching it may conceivably occur at very low densities.

Territory size seems to be influenced by the density of the population. This is true of other species as well, for Spinage (1974) noted that in waterbuck in Uganda the mean territory sizes were 81 ha and 202 ha in areas where the density was one male per 24,3 ha and 56,9 ha respectively.

In Nairobi National Park, Leuthold (1970) estimated the

sizes of impala territories in one of his study areas to range from 0,5 to 0,9 km^2 (mean 0,6), and in the other as from 0,2 to 0,4 km^2 (mean 0,3). The respective densities in these two areas were approximately 13,3 and 25 impala per km^2. In both examples the territory sizes are directly proportional to the densities, suggesting that a correlation does exist between density and territory size. This was also the conclusion reached by Estes (1974).

The overall density of impala in Mkuzi during the study was 74,7/km^2, and the mean territory size measured was 0,066 km^2. This stengthens further the hypothesis that territory size is correlated with population density, despite the fact that in Mkuzi territoriality is strictly seasonal. (During the rutting season of April and May the population density was 73,9/km^2).

There may also be a correlation between territory size and the presence of a very short rutting season in Mkuzi. The presence of a large number of territories within the home range of a breeding herd would ensure greater reproductive success during this short season than would large, scattered territories, with less possibility of encounters between males and females.

During the course of the sampling for territorial males in April and May and at other times over this period, the position of all territorial males seen was noted on a map. With the exception of only a small proportion of them all territorial males were aggregated, albeit well spaced within aggregations. Points at which these groupings of territories

were recorded during road strip sampling are shown in Figure 14. These territorial "arenas" are by no means all that occur in Mkuzi, for the distribution of those shown is restricted to the vicinity of the roads and tracks used in sampling.

The mean number of territorial males recorded in May 1970 and 1971 was 83 (76 in 1970 and 90 in 1971). The mean number of territorial males in the whole of Mkuzi was therefore calculated as 1512 (1385 and 1640) and the density was 6,55/km^2. These figures were then calculated in terms of the three strata and the results are as follows (density in brackets):

	Mean	1970	1971
High	638 (6,74/km^2)	571 (6,03)	719 (7,59)
Medium	503 (6,84/km^2)	485 (5,97)	498 (6,71)
Low	185 (2,60/km^2)	211 (3,41)	150 (2,40)
Total	1 326 (5,75/km^2)	1 267 (5,49)	1 367 (5,92)

It will be shown later (Chapter 10) that adult males comprised 18,4% of the population in May. From Figure 12 it can be seen that 45,5% of all adult males were territorial in May. Thus 8,37% of the population would have consisted of territorial males, giving a mean figure of 1 334 territorial males. This figure is comparable with that obtained by the density method above.

The difference between the densities of territorial males in the high and medium strata is not significant ($P < 0,01$), while the difference between the mean of the

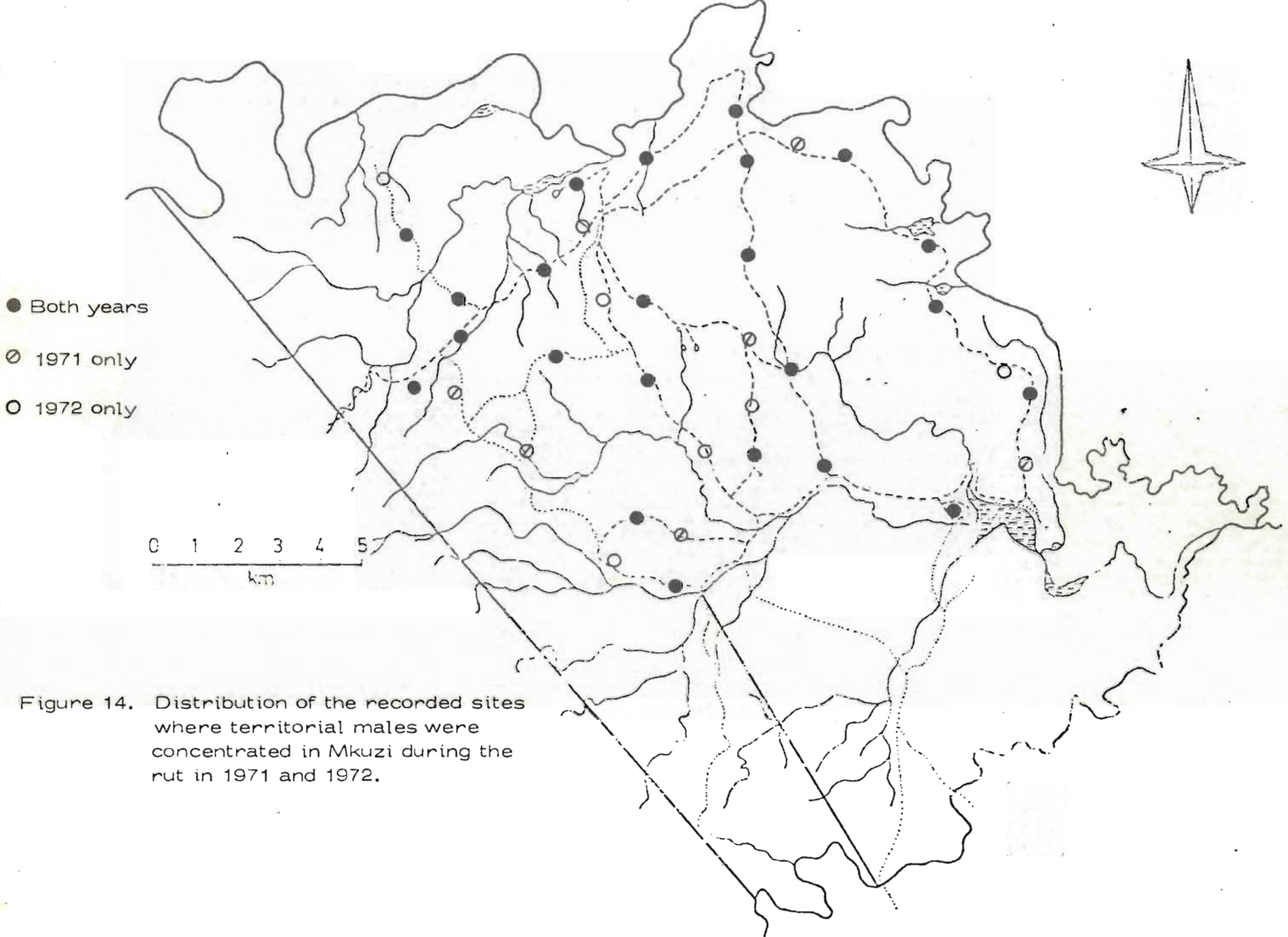

Figure 14. Distribution of the recorded sites where territorial males were concentrated in Mkuzi during the rut in 1971 and 1972.

high/medium strata and the low density stratum is significant ($P > 0,75$). There is therefore a preference by territorial males for more favourable habitat represented by the high and medium density strata.

6.2.4. Bachelor herds.

This herd type is composed of those adult males which are not solitary, of immature males, and of juvenile males. The proportions of each combination of age classes are shown in Table 16.

While no particular seasonal trend is evident from these data, some of the individual figures are important. For instance, the very low proportions of adult male bachelor herds in May and September correspond with the two annual peaks of territorial behaviour. The highest proportions of bachelor herds made up of adults and immatures (63,1%) occurs in September, at a time when animals of about 22 months old voluntarily leave the breeding herds and, because of their gregarious instinct, tend to join up with other males. This in part also accounts for the low proportion in September of herds of adult males only.

In May a high proportion of bachelor herds consisting of immatures only is the result of temporary eviction of these individuals from breeding herds during the rut. They remain at the fringes of the home ranges of the breeding herds, before rejoining them after the rut. The increase in number of herds of immature males in October, November and December is accounted for by their voluntary withdrawal

Table 16. Comparative proportions of each of the combinations making up bachelor herds for each month of the year. (Pooled data for 1970 and 1971 samples).

Month	Adults	Adults + immature	Adults + immature + juveniles	Adults + juveniles	Immature
January	39,2	45,1	-	1,0	14,7
February	49,3	39,9	-	-	10,8
March	33,3	45,6	-	-	21,1
April	44,7	37,7	-	-	22,6
May	2,4	33,6	-	4,8	59,2
June	15,8	46,7	-	2,5	35,0
July	16,1	51,6	4,7	11,5	16,1
August	22,5	38,8	-	-	38,8
September	8,5	63,1	11,5	11,5	5,4
October	21,1	21,1	-	14,6	47,2
November	13,4	23,2	-	16,1	47,3
December	27,1	27,1	-	6,2	39,5

from the breeding herds just prior to parturition.

The individual distance, as explained by Leuthold (1977), is greater between the animals in a bachelor herd than it is between females. This was a common feature of Mkuzi impala, in which the breeding herds maintained close cohesion while feeding and resting. Males on the other hand, were more scattered at all times. The mechanism accounting for this habit is the greater degree of aggression evident between males, even during the non-territorial period. This became more evident with the onset of behaviour leading to territoriality, starting in January, and corresponding to the first phase of territoriality described by Walther (1972). At this time the roaring displays which, as was described in Chapter 5, are a form of aggression, were heard from time to time. Associated with these displays was a tendency for wider spacing and a greater individual distance, as well as sharp reaction to the close proximity of other males and to any form of disturbance, i.e. they were more "on edge".

With the approach of the rutting season, the individual distance increases between males. It culminates in April and May with the typical territorial spacing. Thus there is no definite time that territoriality may be said to become quite distinct - it involves a gradual transition from a bachelor herd situation to one of territoriality.

In this respect, the southern African populations differ from the East African ones in which territorial males are present at all times of the year (Jarman and Jarman 1974). In East Africa there is a continual interchange of territorial

males, with new ones being drawn from the bachelor herds to replace those which for one reason or another lose their territories. The bachelor herd hierachy (Jarman and Jarman 1974) is not obvious during the rut. With the comparatively brief period of intense territorial activity in the southern populations, the males which hold territories do not lose as much condition as they do in other areas, so that there is not the same turnover of territorial males. Apparently, the build-up between January and April serves the same purpose, with the males displaying the greatest dominance eventually gaining territorial status.

The increased aggression between males leading up to territoriality may be linked to physiological changes reflected by the mean testis mass reported by Vincent (1972). Fairall (1972) also associated these changes with changes in behaviour, concluding that photoperiodic changes trigger the release of gonadotrophins, which in turn cause increases in androgenic hormones and changes in behaviour. He went on to add that the demonstrative behaviour of the male - chasing, fighting, and vocalization - acts as a "phychological trigger to bring the female into oestrous".

6.2.5. Breeding herds.

The proportion of breeding herds in the population is consistently higher than that of each of the other herd types, except in May when the number of territorial males is at its highest, and the breeding herds have been fragmented by the chasing and herding behaviour of the males.

96,5% of the herds analysed as "breeding herds" contained adult females; the remaining herds were made up of what are considered to be "aberrant" groupings, such as juveniles on their own or with adult males. Adult females were in fact looked upon as diagnostic of breeding herds. It must be remembered, however, that some of the herds which contained no juveniles (comprising 22,2% of breeding herds) may have been made up of immature females, which are indistinguishable from adults, and which have not in fact bred.

The mean size of breeding herds throughout the year (n = 3 099) was 14,84 (S.D. 5,73), with a range from 9,26 in December to 28,83 in February. The low mean size in December was obtained because the single December sample was taken during parturition, and a large number of females were in small groups. It may thus give a false impression although, of course, this period is an important one, albeit very brief. The trend in sizes of breeding herds is shown graphically in Figure 15, and these data reflect the social dynamics of the female segment of the population.

Just prior to parturition, pregnant females break away from the main-breeding herds, and give birth in isolation. For up to a week after parturition the females remain solitary or form small groups. At this time they are very nervous and, from their condition and disposition, it is assumed that the young are concealed. Occasionally very young, obviously new born lambs, may be seen with their mothers but, for the most part, they do not accompany the females and are presumably "lying out". This observation agrees with that of Jarman and Jarman (1974) except of

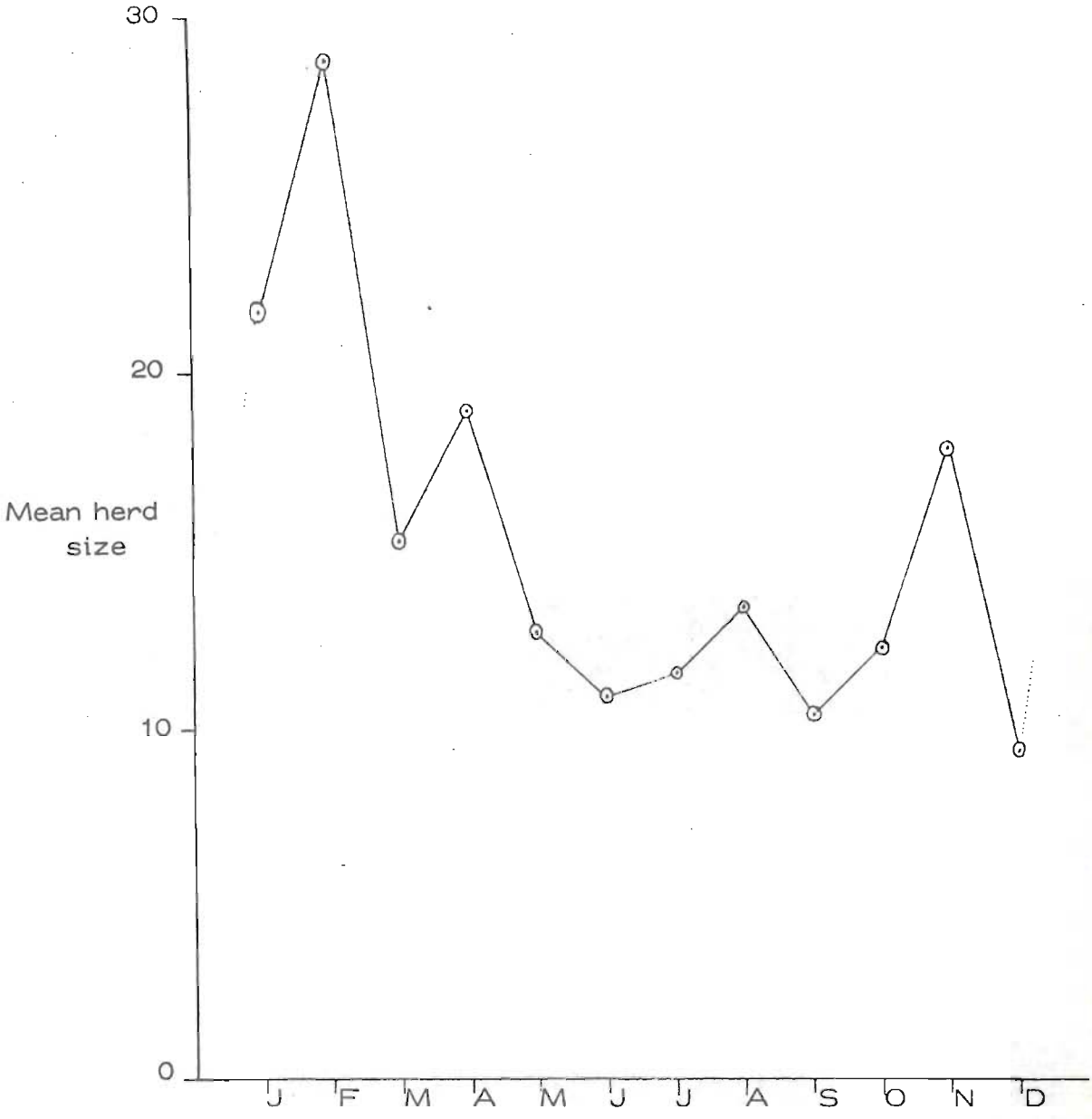

Figure 15. Monthly mean size of breeding herds of impala in Mkuzi Game Reserve. (Pooled data for 1970 and 1971 samples).

course that in the southern populations large numbers of females give birth during a comparatively short period - about two or three weeks - while in East Africa the season of births is not well-defined and young may be born at any time.

The advantages of this very abbreviated breeding season have been discussed by Estes (1974). Apart from herd size serving a directly protective function, the presence of large numbers of juveniles offers the advantage of providing more young than predators can handle. Similarly, for the remainder of the year not enough young are available to sustain a large population of predators. It is not clear why the same seasonal concentration of births has not evolved in East Africa as well.

Jarman and Jarman (1974) add that the period of lying out may be shorter when other juveniles are abroad, but I have no evidence from Mkuzi to verify this.

After a period of comparative isolation the individual females and the small groups join up again, with their young, to form larger herds. This very pronounced tendency to aggregate at this time of the year culminates in February, when the largest herds are encountered. Most of these were recorded in the western parts of the reserve, which have a more open type of vegetation physiognomy. This agrees with the findings of other workers, e.g. Estes (1974), who discussed the correlation between herd sizes and habitat, postulating that the greater ability to maintain visual contact in open country is one of the reasons for large herds. Leuthold (1970) also found that the breeding herds were generally much smaller in the forest than in the open grassland.

In March, April and May the increasing disruptive activities of territory-seeking males have the effect of splitting the herds into smaller ones. The smaller herds enable the territorial males better to control them and to herd them within their territories. Breeding herds of 1 - 5 animals comprised 70% of all breeding herds at this time.

The small size of the herds is maintained throughout the dry winter season when the food resources are at their lowest. This is probably an adaptation to environmental conditions, whereby the smaller herd sizes facilitate foraging by reducing the competition (Jarman and Jarman 1974). The smallest mean size of breeding herds, next to that recorded in December, was 10,3 in September, after which time food becomes more readily available and herd sizes increase.

The tendency to aggregate into large herds during the dry season particularly around water holes, as described by Porter (1970) and by Jarman and Jarman (1974), was not apparent in Mkuzi. This can be seen by the downward trend in the size of breeding herds through the winter, to a low point in September, the end of the dry season (See Figure 15).

6.3. Social development.

Juveniles of both sexes behave in the same social fashion for nearly a year after birth. Initially they are closely associated with their mothers in the large breeding herds

characteristic of the period from late December to March. The creche groups described in Chapter 5.3.8. are made up of both sexes, and social interactions, at least until April and May, are not different between the sexes.

During the rut, the chasing and herding behaviour of territorial males results in fragmentation of the breeding herds, and some of the juveniles may be separated from their mothers. They are then about five months old. This is a critical period for the juveniles for, although some of them may be weaned, and most are able to browse and graze, the social trauma created by the fragmentation results in stress and probably some mortality. They are also particularly prone to predation at this stage. The weaning process in Mkuzi is complete after six to seven months, while in East Africa it ends about a month earlier (P.J. Jarman and Jarman 1973). The tendency for juveniles to become separated and independant was reported also by Dasmann and Mossman (1962a).

6.3.1. Males.

Jarman and Jarman (1974) point out that males leave the breeding herds to join bachelor herds when they are between six and nine months old. This is because they are presumbly looked upon by territorial males as potential competitors, and are therefore subjected to the aggression of these males and forced to leave the breeding herds.

In Mkuzi, most of the juvenile males remain in the breeding herds until they are about nine or ten months old.

There is a tendency, as they get older, for these animals to form sub-groups within the herds and to take increasing part in social interactions among themselves. The commonest such interaction is play-fighting, associated with the development of horns from the age of about four months, and probably also with hormonal changes.

During September and October, the incidence of juvenile males in bachelor herds increases. Some of these juvenile males remain with the breeding herds through the next (successive) period of parturition (at which time they become "immature" males) and even through the whole of their second year. However, most of them are ejected from the herds during the next rut, and they then join up, usually with some adults, to form bachelor herds.

P.J. Jarman and Jarman (1973) found a similar male social development pattern in East African impala; juvenile males are first evicted from the breeding herds at about four or five months of age, and between then and the age of 12 months are permitted by territorial males to rejoin the herds progressively less frequently. After 12 months they are permanently excluded.

Mason (1976) reported that juvenile males are evicted by adult males from the breeding herds about one month before the next lambing season, and suggested that this may have been due to incipient territorial behaviour on the part of the adult males. He did not report whether these young males returned to the breeding herds after parturition as frequently happened in Mkuzi.

Kerr (1965) found that male impala become capable of fertilisation at an age of about 13 months, although he doubted whether, under normal circumstances, they take part in reproduction until they are much older. The testis mass of impala reaches a maximum at between 28 months (Kerr 1965) and about 36 months (Vincent 1972), at which time the animals are fully sexually mature. However, in order to mate successfully in a balanced society, males of most territorial species must hold territories (Leuthold 1977, pp. 220, 239) and Jarman and Jarman (1974) found that in impala most territorial males are "prime age" animals of between 4,5 and 6,5 years old. In the present study, the ages of 14 males which were almost certainly territorial, and which were culled in May 1970 and 1971, confirmed the findings of Jarman and Jarman (1974). Only one of them was 3,5 years old, and two were over seven years old. The ages of these animals were determined by the techniques described in Chapter 8.

Two instances were observed of juvenile (approximately five months old) males attempting to mount females which were presumably either approaching or already in oestrous. Anderson (pers. comm.) also reported one similar incident.

6.3.2. Females.

Juvenile females are apparently a more permanent component of breeding herds than are males. Only a very few instances of juvenile females in the company of anything but at least adult females were recorded in Mkuzi.

There is less tendency among juvenile females to form sub-groups within the breeding herds than there is among the males. They do, however, indulge collectively in various forms of play, in which the juvenile males take part, as well as some of the adults.

As has been described earlier, it is not easy to distiguish juvenile females from older females after the age of 9 months. At all times of the year herds composed of immature males and adult females or of adult females, both without the presence of juveniles, were recorded. It is possible that many of these females may in fact be immature animals which have not yet bred for the first time, and that the herds so formed are what may be described as "adolescent herds". Further study may show that adolescent herds are, at least for part of the year, a further basic herd type, but insufficient conclusive evidence was obtained during this study to show this. Porter (1970) also reported that "...there are small herds of ewes without lambs".

The age at sexual maturity of females varies between individuals. In a very comprehensive study on the reproductive physiology of impala in Kruger National Park, Fairall (1971) did not record any pregnant females among animals in their first year. The percentage of animals pregnant in their second year varied between 0 and 87%. In Rhodesia, Dasman and Mossman (1962b) found 11 out of 13 (85%) animals pregnant in their second year, and again none in their first year. In Zululand I.B. Stewart (unpublished report, Natal Parks Board files) found two juveniles in a sample of 27 to be pregnant, while Vincent (1972)

found indirect evidence for six out of 20 first-year pregnancies; this took the form of the presence of corpora albicantia in animals between 12 and 24 months of age.

In an East African population, Kayanja (1969) found that the minimum age at which conception takes place was about 12 months.

6.4. Environmental influences.

Jarman (1974) discussed at some length the effect of various environmental, as well as specific, factors on social organisation. Amongst the most pertinent points he mentions are the tendency towards large aggregations after parturition, and the fact that territoriality may, to some extent, be influenced by the density of the species.

The most important influences on social organisation within a population are the density, the nature of the habitat, and the season.

6.4.1. Density.

It is not unreasonable to assume that at least all adult males have the capability of establishing territories. However, the area available to these males in which territories may be established is limited by the home range of the breeding herds, which are in turn dispersed according to suitable habitat (Jarman and Jarman 1974). Thus the preferred areas of the

breeding herds become those areas in which males establish territories. In areas of high impala density, there is more competition between males for prime territories, and a greater proportion of males which are relegated to comparatively unsuitable habitat. On the other hand, where the density is low, a stage may theoretically be reached at which all adult males are able to establish territories.

Clearly, therefore, there is a close relationship between the effects of density and of habitat on the social organisation. At a low enough density, where the habitat is suitable - a situation that may occur in dispersal of impala into new areas - there may be no need for territories as such to be established; males could simply establish harem herds on the basis of dominance status. Such a situation has been reported by Mason (1976) for a very low-density (0,02/ha) population.

6.4.2. Habitat.

The effects of habitat on social organisation are wider ranging than those of density. Apart from the effects just mentioned, physiognomic differences in vegetation influence the size of the herds. Estes (1974) and Jarman (1974) discuss an apparent correlation between herd size and habitat, stating that larger herds are characteristic of species or populations that occur in open habitat. This is not a general rule, for there are open country species, e.g. oribi Ourebia ourebi and grey rhebuck Pelea capreolus, that occur singly or in small groups. However in species which may occur in both open and closed woodland, e.g. blue wildebeest and impala, the herd size may differ

between the two habitats.

Thus, in the present study, the mean size of breeding herds throughout the year in the more open, western parts of the reserve was 17,4, whilst in the more thickly wooded central and eastern parts it was 12,2. Although the difference is not significant ($t = 0,579$, $d.f. = 22$), the obvious tendency confirms the findings of Leuthold (1970) who found that during his study period 56,6% of breeding herds in his "Forest Area" consisted of between 6 and 25 animals, whilst in the more open "Somali Ridge" 69,3% of herds contained more than 25 animals.

In the case of male/bachelor herds, Leuthold (1970) found a greater incidence of larger herds in the open area than in the forest area. In Mkuzi the mean size of bachelor herds was 5,1 in the west and 4,1 in the centre and east. Again this difference is not significant ($t = 0,851$, $d.f. = 22$).

13,5% of all males in the western area were territorial, whilst 21,1% in the centre and east were. The respective figures for the May peak of territorial behaviour were 30,0 and 53,8. It is quite clear, therefore, that there is a preference on the part of territorial males for the more thickly wooded areas. The reason for this is not clear, although it may be related to the nutritive value of the browse in that part relative to the grazing in the west. There is also an association between the higher incidence of territorial males in the east and the smaller size of the breeding herds, particularly during the rut, when the mean is 7,7 compared to 15,5 in the west. This is explained by the greater

disruptive influence of the higher concentration of territorial males in the east.

6.4.3. Season.

The seasonal changes in each of the herd types have already been described in discussing the herd types themselves, but it is important to emphasise the effects of the seasonal nature of breeding of impala in Mkuzi. It is this feature, more than any other, which influences the social behaviour.

Following the break-up of the breeding herds during the rut (from a maximum mean size of 28,8 in February to 12,7 in May), the following dry season results in a continuing drop in mean herd size to 10,3 in September. The reason for this is competition for the comparatively small amount of available high-quality forage, particularly towards the end of the dry season, which extends from April through September in a normal year. With the onset of spring rains in October the herds again increase in size, and continue with this trend, with the exception only of the short period when parturition takes place, usually during the last week of November and the first week of December, when small groups of adult females occur.

There is no significant seasonal change in the mean size of bachelor herds, whilst the incidence of territorial males is of course very seasonal. The onset of territorial behaviour in the southern populations of impala is thought to be triggered by the photoperiodic conditions (Fairall 1972), acting through hormonal changes. This seasonal incidence of

territorial behaviour can be compared with the situation in East Africa where there is no marked change in day length, and where territoriality occurs throughout the year, e.g. Jarman (1976). Whether it is the territorial behaviour of the males which induces the onset of oestrous in males or whether the two have become synchronised through natural selection is unknown. Evidence provided by Vincent (1972) shows that follicles are produced in the ovaries at all times of the year, whilst Fairall (1971) showed that testicular activity also occurs throughout the year. This seems to suggest that there is a psychosomatic effect on the female physiology caused by the behaviour of the male and which is in turn induced by photoperiod. Alternatively, a silent oestrous as observed by Watson (1969) in wildebeest, and of which some evidence was found in impala by Vincent (1972), may stimulate increased male activity. Fairall (1970) estimated the oestrous cycle to be 19 or 29 days, which would give ample time for territorial behaviour to build up to the climax and to synchronise with the oestrous period.

Sinclair (1977) suggested that there may be a correlation between conception and the lunar cycle in buffalo. If this is true of impala then it may account for the synchrony of breeding in southern populations.

6.5. Species interactions.

It is not always easy to single out any one influence on social behaviour, but the effect of individual or group behaviour on other animals in a gregarious species such as impala may

be considerable in certain circumstances. Many of these interactions and their effects have already been described, but others remain to be discussed.

Among these are the changes in social structure of the two herd types which involve more than one animal. Table 16 demonstrates the dynamics of bachelor herds, highlighting particularly the increase in the number of these herds consisting of immature males alone during the rut, when they are chased out of the breeding herds. There is another increase in the incidence of immatures when these animals are approaching two years of age. At this time they voluntarily leave the breeding herds, and do not rejoin them again. Very few juvenile males leave the breeding herds during their first year; this is in contrast to the situation in East Africa, where most of the males have left the breeding herds by the end of their first year. Again this is an effect of year-round territoriality, with the territorial males keeping any potential competitors out of their territories.

The occurrence of very large breeding herds in late summer is probably associated with the need for security for the very young. Estes (1974) pointed out the importance of the herd to the well-being of gregarious bovids, and the fact that in these species the herd takes the place of cover. On the other hand, it will be remembered that impala may conceal their young, at least for a short period. This indicates a transitional stage between the concealed young typical of solitary antelopes such as duiker and reedbuck,

and the precocial young of highly gregarious antelopes such as the Alcelaphini. The formation of creche groups in very young impala may be looked upon as a social form of "lying out". These groups are formed in much the same way as the young are concealed by solitary antelope, which also occurs following a period of nursing (e.g. Fichter 1974). Lent (1974) points out that maternal isolation behaviour during parturition, which includes the maintenance of isolation for a period after parturition, must not be confused with "hiding" behaviour. If it is accepted that creches are a form of lying out, then the impala does indeed represent an intermediate stage.

6.6. Discussion.

The seasonal nature of impala breeding in Mkuzi clearly influences the patterns of social behaviour, and creates differences between this southern population and those which have been extensively studies in East Africa. In this latter area, reproduction takes place throughout the year, although peaks in parturition are evident (Kayanja 1969, Jarman and Jarman 1974). Because reproduction does occur at all times of the year, albeit at different intensities, the social behaviour of these animals must remain geared to this activity, in contrast to the southern populations, where a single peak gives way to behaviour unrelated to reproduction.

Probably the most significant, and certainly one of the most important, patterns of social behaviour in impala, particularly in so far as population dynamics are concerned, is territoriality. It is a year-round occurrence in East Africa, and a seasonal one in southern Africa, although

Mason (1976) has suggested that there was some territorial behaviour from October onwards. In both areas it is closely associated with reproduction and indeed appears to be a prerequisite to mating.

The nature of territoriality has been debated at length. It can only be looked upon as a concept and cannot be defined because of the various forms it takes in the animal kingdom. Leuthold (1970) laid down five criteria, several or all of which must be fulfilled before a population can be described as exhibiting territorial behaviour. Later, Leuthold (1977) discussed the term "territory" in some detail, and after reiterating that "...it is virtually impossible to arrive at an all-embracing definition" (p. 192), went on to provide a compromise: "A territory is a spatially fixed area within which a given animal consistently prevents certain other individuals from engaging in certain activities" (p. 193). The variants in this definition are the "given animal", "certain other individuals", and "certain activities".

In the context of impala territoriality, the given animal is a territorial male, the other individuals are other adult males, and the activity is mating with females.

Walther (1972) described three types of territory:

1. The pair territory.
2. The individual territory.
3. The mating territory.

These were recognised by Estes (1974) and Leuthold (1974). It is quite obvious, since the impala is a gregarious species, that its territory is of the third type. Furthermore, because mating

in the southern populations is so strictly seasonal, males hold their territories mainly during this season.

Leuthold (1977) described the various types of territory in more detail, and placed the impala in his type 5a - the "normal" mating territory. He also acknowledged that under certain conditions, such as an isolated population described by him (Leuthold 1970), impala may adopt a "harem" system, with one male monopolising a herd of females, whilst under conditions of high density, certain antelope may develop an arena, or lek, system. It is this latter situation which is very nearly achieved in the Mkuzi impala population, falling somewhere between having the normal mating territory and the arena territory, with a number of contiguous territories in a fairly restricted area, separated from other similar "arenas" by quite large distances.

The situation described by Mason (1976) in which low intensity territoriality was exhibited from October onwards may in fact have been one approaching a harem system, since the density in his study area was very low.

Territoriality is important in various aspects of the population dynamics of a species, and the most obvious ways in which it plays a part are:

(i) Spinage (1974) points out that the number of males decreased relative to the number of females as the density of a waterbuck population increased. This is because territories can only be compressed to a limited extent, so that surplus males must disperse. This situation would pertain also in impala, with bachelor males being forced

out of the population, as was found by Hitchins and Vincent (1972).

(ii) The existence of territoriality makes for more effective reproduction, in that mating can take place under undisturbed conditions, with males having virtually exclusive rights to oestrous females while they are in their territories. This obviates disruptive competition from other males, and favours a high natality rate.

(iii) The fact that bachelor males which are unsuccessful in establishing territories, including the younger males, are forced to disperse into less favourable habitat, may well be the cause of the inequality in the sex ratio in most gregarious species which are territorial.

(iv) The spacing out of territorial males, and the corresponding sizes of the breeding herds, act as a means of ensuring that overutilisation of the habitat does not occur. Closely-spaced territories necessitate small breeding herds if the males are to be able effectively to contain them. On the other hand, large territories enable breeding herds to remain intact, because there is less disruption.

Finally, it is postulated that the temporary territorial "arenas" which are a feature of Mkuzi Game Reserve are created in one of two ways:

(i) They are centred on the home ranges of breeding herds, or

(ii) They are the equivalent of "bachelor herds" in which the individual distance has become sufficiently large as to create separate territories. Bachelor herds are not stable social groupings so that one or more herds may combine to create an arena. In other words males may, in a sense, be territorial at all times, although for most of the year their

territories are small, mobile, poorly defended, and restricted simply to the "individual distances".

In fact the arenas are probably created as a result of a combination of these two methods.

CHAPTER 7.

DISTRIBUTION

7.1. Introduction.

Several factors were thought to influence the distribution of impala in Mkuzi Game Reserve, for casual observations over a number of years have led resident staff there to note changes in patterns of concentration and of movements. Among those factors which it was possible to examine in this study were vegetation, water, seasons, and sex and age classes.

In discussing the physical features of Mkuzi Game Reserve, and in particular the soils (Chapter 2.2.), mention was made of three broad subdivisions of the game reserve, namely the Lebombo mountains and foothills region influenced by their geology; the western lowlands, predominantly west-facing with mainly red soils; and the eastern lowlands, predominantly east-facing with grey to brown, more clayey soils. The vegetation associations are very closely linked with the soil types, although the physiognomic features may vary within each soil type.

7.2. Methods.

The three natural ecological subdivisions of the reserve were used as a basis for dividing the reserve into six broad regions for the purpose of analysing gross movements of impala.

Each one was further subdivided, so that a total of six regions was obtained as illustrated in Fig. 16. This north/south division was done as nearly as possible according to the drainage patterns.

During the course of the road strip sampling the locality of each impala or group of impala was recorded according to the vehicle odometer. In this way it was also possible to analyse the distribution according to vegetation type and to the regions described above. Because the composition of each group according to sex and age class was also recorded, this made it possible to analyse distribution separately for each of these classes.

As discussed earlier (Chapter 4.3.2.) the physiognomic vegetation types were also used in determining the strata for population estimation and, because of the high porportion of impala recorded in the high density stratum, this was subdivided into the Acacia woodland and broadleaf woodland to permit further analysis of distribution according to this factor.

7.3. Results and discussion.

7.3.1. Distribution according to vegetation types.

If there is any one single factor which, on a year round basis, has any influence on the distribution of impala, it is the vegetation. Food and cover are the two most important requirements apart from water. In Mkuzi the three basic physiognomic types consist on the one hand of upland open

woodland, which may provide some food and little cover and, on the other hand the thicket, which provides adequate cover but little food, whilst in the middle are the various lowland open to closed woodlands, which provide both food and cover in adequate quantities.

Reference to Tables 10 and 11 demonstrates that there was a decidedly higher number, and indeed density, of impala sampled in what has been termed the "high density stratum". This consists of the open to closed woodlands, occuring mainly in the lowlands, and it is concluded therefore that the distribution of impala is influenced by the distribution of the vegetation.

The proportions of the calculated numbers of impala in each stratum and those of the numbers actually sampled are shown in Table 17, together with the numbers that would be expected if the distribution was random and uniform over the whole of the inhabited portion of the reserve. This excludes the unutilised upland grassland. The significance of the differential distribution is further shown by the analysis of variance in Table 12. A test of the significance of difference between the sampled and expected populations in each stratum is provided in Chapter 4.3.3.3.

The numbers and the relative proportions of impala recorded in the Acacia woodland compared to the broadleaf woodland (the subdivisions of the high density stratum) are shown in Table 18. These results may be compared with the fact that 81,6% of this stratum sampled consisted of

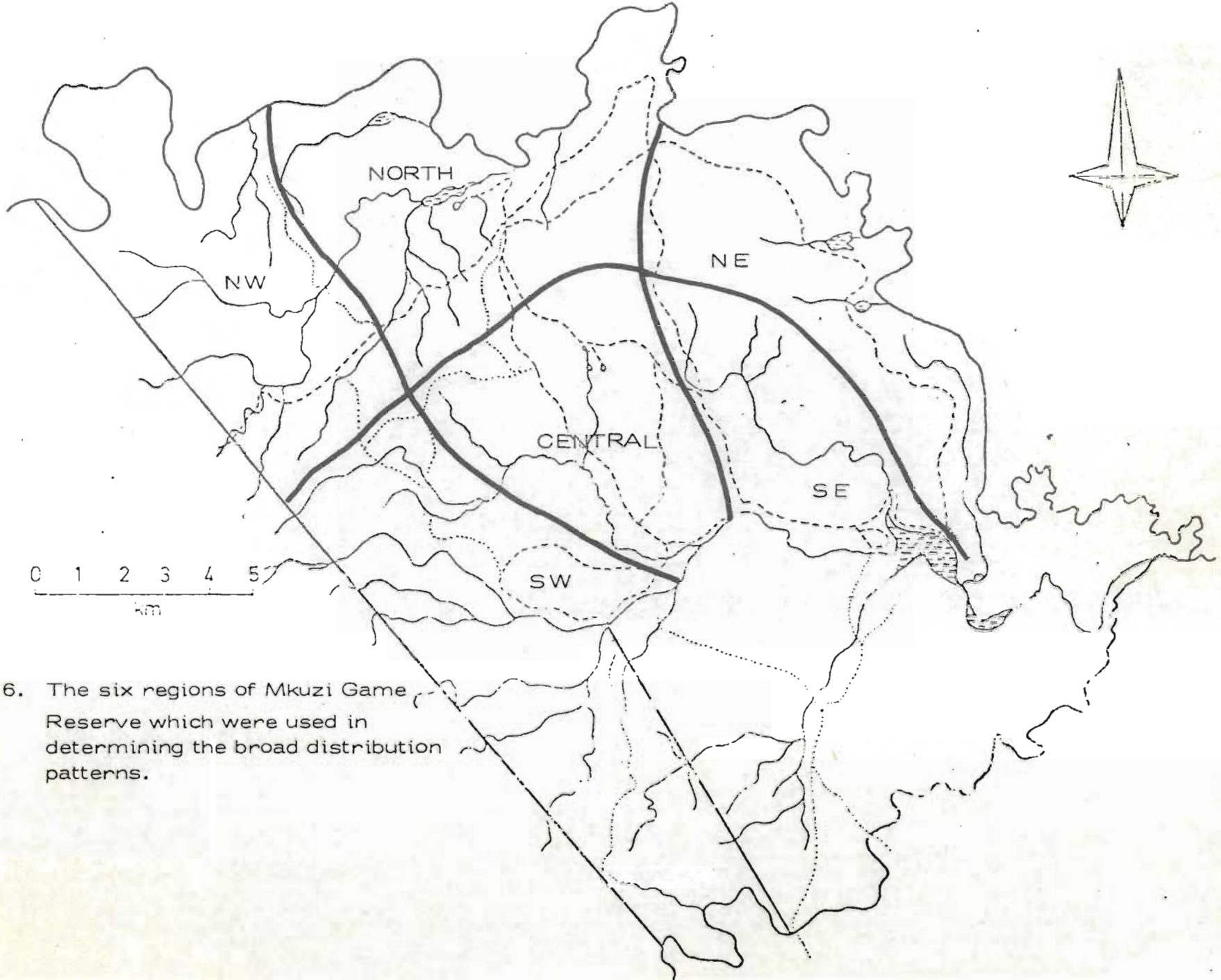

Figure 16. The six regions of Mkuzi Game Reserve which were used in determining the broad distribution patterns.

Table 17. The relative proportions of the total inhabited area of Mkuzi in each stratum and of the numbers of impala seen, and of the calculated and expected populations in each stratum in 1970 and 1971. The "proportions" of expected populations are those that would be expected if impala were evenly distributed over the whole reserve.

Stratum	% of total area sampled			% of total numbers seen			% of calculated population			% of expected population		
	H	M	L	H	M	L	H	M	L	H	M	L
1970	70,3	24,4	5,3	82,2	16,1	1,7	61,6	27,2	11,2	41,0	32,1	26,8
1971	70,3	24,4	5,3	82,5	15,0	2,5	60,0	24,6	15,4	41,0	32,1	26,8
Both years				82,3	15,6	2,0	60,9	26,0	13,1			

Table 18. The numbers of impala and the relative percentages sampled in the Acacia and broadleaf woodland of the high density stratum respectively. Separate data for the 1970 and 1971 samples are shown together with the mean.

Month	1970				1971				Mean			
	Acacia woodland		Broadleaf woodland		Acacia woodland		Broadleaf woodland		Acacia woodland		Broadleaf woodland	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
January	1 243	81,6	281	18,4	1 007	81,8	224	18,2	1 112,5	81,5	252,5	18,5
February	1 056	87,8	147	12,2	885	84,8	159	15,2	970,5	86,4	153	13,6
March	672	80,2	166	19,8	911	83,5	180	16,5	791,5	82,1	173	17,9
April	825	84,4	153	15,6	878	86,2	141	13,8	851,5	85,3	147	14,7
May	696	81,6	157	18,4	734	84,8	132	15,2	715	83,2	144,5	16,8
June	647	82,1	141	17,9	848	82,7	177	17,3	747,5	82,5	159	17,5
July	611	84,2	115	15,8	800	84,3	149	15,7	705,5	84,2	132	15,8
August	547	84,3	102	15,7	755	86,8	115	13,2	651	85,7	108,5	14,3
September	658	74,4	227	25,6	638	79,7	162	20,3	648	76,9	194,5	23,1
October	681	73,5	246	26,7	653	81,5	148	18,5	667	77,2	197	22,8
November	854	78,2	238	21,8	875	78,7	237	21,3	864,5	78,4	237,5	21,6
December	985	78,2	275	21,8					985	78,2	275	21,8

Note: 81,6% of the high density stratum sampled was Acacia woodland and 18,4% was broadleaf woodland.

predominantly Acacia woodland, and 18,4% of predominantly broadleaf woodland. Thus in the period from February to August, there was an apparent preference by impala for the Acacia veld and this preference switched to the broadleaf woodland between September and December. This trend was consistent in both years.

The conclusion to be drawn is not evident from the data available for there are insufficient data on the dominant species composition of the two vegetation types. Whilst it is tempting to postulate on the fact that Acacia spp. provide the necessary dietary requirements for all but the early summer season when the broad-leaved plants are most succulent, there may well be other factors such as the herbaceous plants which may play a more important part in habitat selection.

7.3.2. Distribution according to water.

In the earlier discussion on the distribution of water in Mkuzi Game Reserve (Chapter 2.3.) it was stated that the only really permanent surface water during the period occurred in the central region, where water is artificially supplied to two pans with game-viewing hides. A small quantity was available in the gorge, but to reach it would have involved walking a long way up the river bed. Most of the animals in the reserve therefore undoubtedly used the central region's supply.

During the summer months, from the advent of the first good rains in October through to about July, by which time all other surface water had disappeared, there was generally ample water in the numerous pans and drainage lines scattered

about the reserve. Certainly the numbers of animals using the artificial waterholes was very small indeed until mid-July.

The distribution of impala within a radius of 5 km from the water was used as a criterion to test the effect of water, assuming that the only water available in July, August and September was at Bube and Msinga pans. Because it was possible to locate impala that were recorded in the road strip sampling to within about 200 m, the results of this sampling were analysed to locate the animals to inside or outside the 5 km radius. The results of this analysis are shown in Table 19, from which it can be seen that there is no real difference in impala distribution in relation to the permanent water, according to the season.

The conclusion is that impala in Mkuzi are not influenced in their distribution by the limitation of the water, and that they are either not completely dependent on surface water for daily requirements or that they will move more than 5 km to drink.

7.3.3. Regional distribution.

The distribution of impala in Mkuzi Game Reserve was next analysed according to the six broad regions shown in Fig. 16. This analysis is shown in Table 20, and illustrated in Figure 17 (a) and (b).

Certain trends can be seen from these results:

a. A sharp, brief drop in the population of impala

Table 19. The mean monthly percentages of impala recorded within 5 km of Bube and Msinga pans compared with the percentages recorded farther than 5 km away.

Month	Less than 5 km	More than 5 km
January	64,2	35,8
February	59,5	40,8
March	53,8	46,2
April	64,2	35,8
May	62,5	37,5
June	62,7	37,3
July	68,3	31,7
August	59,8	40,2
September	58,0	42,0
October	57,1	42,9
November	60,8	39,2
December	68,4	31,6

Table 20. The number of impala sampled in each month in each region of Mkuzi Game Reserve, expressed also as a percentage of the total sampled in that month. The figures used are the mean of the two years of the totals of the two daily counts in each sample.

Month	Region / Total	NW		SW		N		Central		NE		SE	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
January	3 190	370	11,6	1 260	39,5	402	12,6	536	16,8	262	8,2	360	11,3
February	2 779	392	14,1	633	22,8	390	14,2	692	24,9	496	17,8	170	6,1
March	2 438	378	15,5	505	20,7	390	16,0	622	25,5	416	17,1	127	5,2
April	2 467	444	18,0	566	22,9	429	17,4	614	24,9	264	10,7	150	6,1
May	2 106	105	5,0	842	40,0	206	9,8	628	29,8	152	7,2	173	8,2
June	2 217	357	16,1	592	26,7	326	14,7	479	21,6	328	14,8	135	6,1
July	2 103	360	17,1	656	31,2	292	13,9	341	16,2	233	11,1	221	10,5
August	1 883	290	15,4	286	15,2	273	14,5	471	25,0	281	14,9	282	15,0
September	2 086	217	10,4	455	21,8	281	13,5	457	21,9	321	15,4	355	17,0
October	2 172	224	10,3	399	18,4	387	17,8	616	28,4	261	12,0	285	13,1
November	2 577	268	10,4	742	28,8	402	15,6	639	24,8	314	12,2	212	8,2
December	2 870	450	15,7	886	30,9	307	10,7	760	26,5	215	7,5	252	8,8

Areas sampled: NW 198,95 ha; SW 331,47 ha; N 227,52 ha; Central 289,87 ha; NE 112,95 ha; SE 105,78 ha

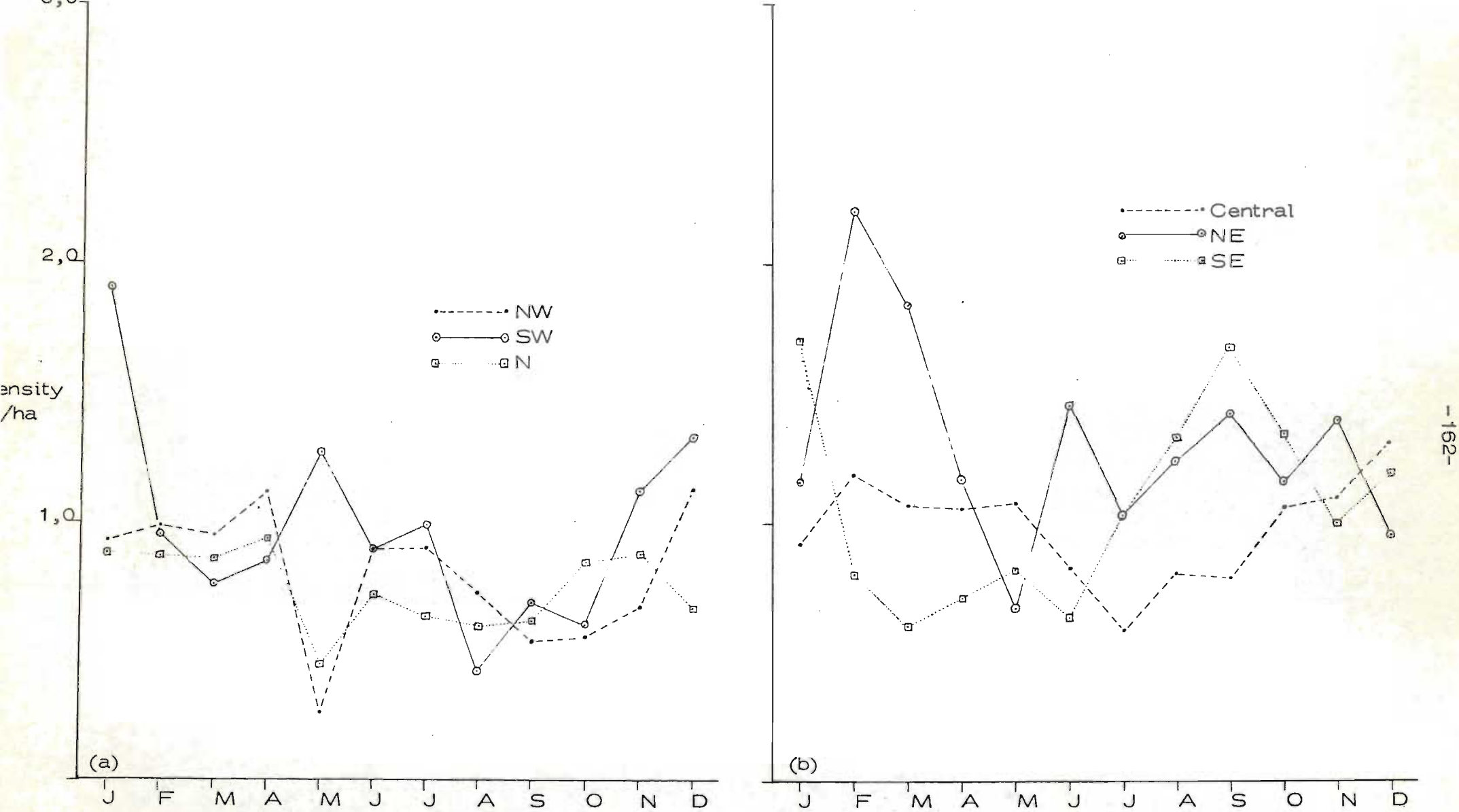

Figure 17. The densities of impala sampled in each region of Mkuzi through the year (mean for 1970 and 1971) expressed in animals per hectare.

in the north-west in May. This coincides with the rut, which may have some bearing on it. However, the density of territorial animals recorded in May in the north-west region was 10,30/km^2, compared to 5,90/km^2 over the rest of the reserve.

b. Coinciding with the decrease in proportion of impala in the north-west, there was an increase in the south-west, where the density of territorial males was 6,64/km^2 compared to 6,58/km^2 elsewhere.

c. There was a substantial increase in the porportions present in the south-west in November, December and January, coinciding with the periods of parturition and when lambs were up to three months old.

d. A decrease in the proportions in the north-east region in December and January, and again in May.

e. An increase in the proportions of impala in the south-east from July to September, dropping again until January.

f. The mean size of breeding herds in the north-west region in May was 5,7 compared to a mean of 12,5 for the whole reserve. The difference is significant:
chi square = 3,699, $P<0,05$.

The conclusions to be drawn from these results are:

(i) The densities of territorial males relative to those

of all impala in the north-west and south-west regions suggests that the density of animals in an area has no effect on the territorial drive of males. Even in the north-west where the overall density was low, there was a higher density of males. However there is no information on the sizes of individual territories in this region for comparison with the data presented in Chapter 6.2.3.

(ii) The south-west is a favoured region for parturition. The reason for this may lie in the fact that this region consists of a mosaic of vegetation types, dominated by woodland, but interspersed with small patches of thicket. This latter provides the cover which may be necessary when the lambs are very young.

(iii) The north-west region contains a high proportion of very favourable impala habitat, but for some unknown reason it is not preferred in the midsummer months. The heat and humidity in January may reach intolerable levels, because of the flatness of the terrain and the lack of air movement. This may in turn affect the impala, but no data on tolerance limits of the species are available.

(iv) The increase in the proportion of animals found in the south-east coincides with a drop in the overall density of impala throughout the reserve. It is consequently thought to be associated with temporary local movement out of the reserve onto Nxwala State Land. A general south-eastward movement takes place starting in July, and because Nsumu pan was dry during the two years of the study, it was possible for impala to cross over both through the pan and across the

drainage line which feeds it.

(v) The increase in the south-west region in particular in November suggests that there is a return of animals from Nxwala at this time, just prior to parturition, while the fact that there is an associated increase in the proportion of females in the population at this time implies that this category is largely responsible for the local movement.

(vi) The smaller size of breeding herds in the north-west in May, when there is a high density of territorial males, accords with the conclusion in Chapter 6.6 that closely-spaced territories necessitate smaller breeding herds in order that males can more effectively control the females.

7.3.4. Seasonal distribution.

Figures 9 and 10 show that a distinctly larger number of impala was sampled during the wetter summer months from October to March inclusive than in the period April to September. The mean monthly sample size during the wetter months was 2671 (S.D. = 199) and during the drier months it was 2143 (S.D. = 140). The difference is not significant: $t = 0,894$, d.f. = 10, and $P > 0,2$.

The relative proportions of the samples in each region are shown in Table 21, from which it may be seen that a higher proportion of the population was recorded in the wet season in all regions of the reserve.

Again there is a slight increase in the dry season as a

whole in the proportion of animals recorded in the south-east as well, this time, in the north-east. The reason for this may lie in the fact that the vegetation in these regions holds its moisture for longer because of the nature of the soils and the comparatively poor drainability, thus rendering the browse more favourable. It also lends more evidence to the southward movement of impala late in the dry season.

7.3.5. Distribution according to sex and age.

The distribution of the various sex and age classes of impala in Mkuzi according to the density strata is shown in Table 22.

There was a fairly consistently higher proportion of females and juveniles in the high density stratum throughout the year than of males, suggesting that the quality of the habitat is more important to females than to males. The lowest proportion of males in the high density stratum was in May, which is consistent with the fact that males select territories in this stratum, forcing non-territorial animals into other areas.

The highest proportion of females in the high density stratum was in December and January, when the lambs are small and there is a need for a high level of nutrition while the females are lactating.

It will be shown later that there was a drop in the proportion of females present in the reserve in August and September. This suggests that the outward movement which,

Table 22. The number of impala seen per month in each stratum of Mkuzi Game Reserve, according to sex and age, expressed as a percentage of the total of that category seen.

Category	Stratum	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
Adult male	H	79,3	74,6	76,1	72,4	71,7	72,9	74,9	76,4	83,8	82,5	86,7	84,4	79,1
	M	15,1	20,1	21,7	19,2	18,4	15,6	15,7	16,8	11,5	11,6	8,2	10,9	13,1
	L	5,6	5,3	2,2	8,4	9,9	11,5	9,4	6,8	4,7	5,9	5,1	4,7	7,8
Adult female	H	87,6	77,0	80,4	81,1	79,9	84,6	80,9	75,4	76,2	79,4	87,2	88,1	83,9
	M	7,5	18,8	15,2	13,7	18,6	12,8	11,4	15,6	18,1	16,2	7,9	5,7	12,2
	L	4,9	4,2	4,4	5,2	2,5	2,6	7,7	9,0	5,7	4,4	4,9	6,2	3,9
Imm. male	H	71,2	65,7	72,7	74,9	70,2	76,4	79,5	81,2	81,9	82,0	80,2	75,2	77,7
	M	18,7	21,2	18,4	16,0	17,6	16,1	15,3	16,4	15,7	12,7	15,5	14,9	14,2
	L	10,1	13,1	8,9	9,1	12,2	7,5	5,2	2,4	2,4	5,3	4,7	9,9	8,9
Juvenile	H	91,2	84,5	82,5	80,2	81,4	85,7	84,8	79,9	81,5	82,2	75,4	84,3	84,6
	M	5,6	7,9	11,4	15,3	14,1	11,4	12,1	13,4	7,4	7,9	15,6	14,0	12,2
	L	3,2	7,6	6,1	4,5	4,5	2,9	3,1	6,7	11,1	9,9	9,0	1,7	3,2

as has been described above, took place at the same time, may be mainly of females. Again the fact that females were apparently responsible for the rise in density in November, confirms this. It was in the south-west that the highest proportion of lambs was sampled in December/January - 39%, against the next highest in the central region of 27%.

In order to check the hypotheis that females are mainly responsible for the movement, two sample counts were carried out on Nxwala State Land, using the same routes, in March and September 1971 respectively. The results are shown in Table 23.

Although the samples are not large, the trend is quite clear: a much higher proportion of adult females was found in September, with a correspondingly lower proportion of other categories, and there was a greater overall density. Taken together, these two observations provide more evidence of a seasonal influx to Nxwala, which is dominated by females.

7.3.6. General discussion.

The whole question of impala distribution in Mkuzi must be related to two factors: the habitat requirements under different environmental conditions, and the tendency towards sedentary or nomadic behaviour in the species.

Earlier discussion revealed that in Mkuzi, the impala are only partially dependent on surface fresh water. Where water is readily available, impala will utilise it, but evidence does indicate that they are equally able to subsist, for unknown

Table 23. The numbers of impala seen in two sample counts carried out along a fixed route on Nxwala State Land in 1971.

Category	March		September	
	No.	%	No.	%
Adult male	77	21,4	108	14,7
Adult female	135	37,5	457	62,1
Immature male	32	8,9	21	2,9
Juvenile	116	32,2	150	20,4
Total	360		736	

periods, without water. Lamprey (1963) recorded impala 40 km from the nearest surface water, commenting that the dew was probably adequate to sustain them. This does not seem to be a general rule, however, for Western (1975), in studying a population not far removed from that of Lamprey, did not record impala farther away than 8 km from water in the dry season. In Mkuzi Game Reserve, no part of the reserve is more than about 10 km from permanent water and, although no direct evidence is available, it is suspected that animals in even quite distant areas moved to the water, if not every day, then at least infrequently. The numerous trails, and observations of impala using them, support this idea. Be that as it may the water factor is probably not one which significantly affects impala distribution and movement in Mkuzi Game Reserve.

More important in this regard is the availability of suitable and sufficient food. Jarman (1972) showed that in the Zambezi valley there was considerable seasonal movement of several species of large mammals, including impala, and that this was coordinated with the vegetation types and the availability of food. In the same way, Lamprey (1963 and 1964) also concluded that impala movements into and out of his study area in Tanzania were related to food requirements and availability.

On the question of the distances over which impala move seasonally, Dasmann and Mossman (1962) cited evidence for movements of up to 15 miles (24 km) in the case of individual adult males, but on a population basis, they did not appear to move more than about 5 miles (8 km). They concluded that

impala tend to occupy relatively small home ranges. In East Africa, Jarman (1970) found that even in an exceptionally dry year the maximum recorded distance over which an impala moved from its customary home range was 9,4 km. Furthermore, upon normal conditions returning, all the known impala returned to occupy exactly the same areas as before. This applied to all sex and age categories, but was particularly evident in lone males, which were very relectant to leave their territories.

Leuthold (1970) also showed that the distances normally covered by impala are not great, and that the average size of home ranges was about 4,5 km^2 in males and slightly larger in females, but that both were considerably larger than the territories of individual males. His study was carried out during "normal" seasons, but he added that "under unfavourable environmental conditions the normal home range may be extended to include areas offering a better food supply".

Nothing of what was found to take place in the Mkuzi population is at variance with the findings and conclusions of other workers, although there are no data on individual animals. However, data from this study do provide evidence for the seasonal local movement of impala out of the study area towards the end of the dry season, and a return of at least some of the animals at the start of the wet season, just prior to parturition.

The extent of this movement is difficult to assess accurately, largely because of the capture of a certain number of animals in each of the years during which the

census was carried out. The details of the capture, which was designed as part of the management programme to reduce the population, are as follows:

1970	May	21		
	August	1 044		
	September	309	Total	1 374
1971	May	1 740		
	June	408	Total	2 148

In addition to these, 288 were shot in 1970 and 449 in 1971.

Both capture operations took place over the whole reserve, although not strictly randomly, and it is considered that any influence on the density of any one region was not great: the effect was an overall one. Reference to Figure 9 will show that the effects of the 1970 capture were not reflected in the census results, although those of the 1971 capture appeared to have been evident in May, with at least a partial recovery in June. Nevertheless, the trend in both years was a downward one until August/September in any event, and this trend has been interpreted as indicative of outward movement.

The proportions of the various sex and age classes that apparently leave the reserve will be discussed in a later section.

Seasonal local movement such as has been described, must not be confused with the phenomenon of population dispersal, which combines the need for surplus animals to move out of well populated areas to seek suitable habitat

elsewhere, with the colonisation of uninhabited regions. Dispersal in a nearby population of impala has been described by Hitchins and Vincent (1972), who found that males and non-breeding females are the first to colonise new areas. This was not evident from observations in Mkuzi, although it may have taken place, and been masked by the more general, local and seasonal movements that have been described. The disturbance created by surrounding agricultural activity prevented movement in any direction but southwards, where impala already occurred, so that dispersal and colonisation was not a feature of the Mkuzi population.

The patterns of movement of impala in Mkuzi may be compared with those in the Zambezi valley (Jarman 1972) and in a transitional area between highveld and bushveld in the Transvaal (Mason 1976).

In the Zambezi valley impala showed marked differences in movement patterns between sections of the population. During the wet season from November to April, all impala left the flood plain and moved into the deciduous woodlands. As the dry season progressed, there was a return to the flood plain, and Jarman (1972) reported that this move contained "an above average proportion of males" as forerunners. He concluded that females retain a preference for the broad-leafed woodland throughout the dry season while males showed none towards the end. Furthermore the non-breeding sections of the population (males and immature females) showed less significant preferences for particular habitats than did the breeding sections, whilst breeding sections showed changes in

preference earlier in the dry season than did non-breeding sections.

Whilst the situations in the Zambezi valley and Mkuzi are not directly comparable, there is clearly the similarity that different population sections exhibited different responses to environmental and habitat changes. The extremes in environmental change in the former area are far greater than in Mkuzi, so that the responses of the impala population might be expected to be different. In fact in Mkuzi, there is evidence in Table 23 to indicate that, although the female section was responsible for most of the movement, most of the females were apparently non-breeders, a situation similar to that in the Zambezi valley.

Mason (1976) reported on the seasonal movements of a small population of impala and found that in the dry season three quarters and half of the females and males respectively moved out of a deciduous woodland into an Acacia woodland. Again this indicates a greater mobility of females, although there is no indication of whether these were breeding or non-breeding animals.

CHAPTER 8.

AGEING

8.1. Introduction.

The accurate determination of age is an essential requirement in the study of several aspects of the population biology of animals, for instance, rate of growth, age at sexual maturity, longevity, productivity, and survival and mortality rates. These population parameters are, in turn, essential for the conservation and management of species and populations, whether it be for economic gain (tourism, sport hunting, or game ranching), or for the benefit of the habitat.

For this reason, a great deal of attention has been given by wildlife biologists to various techniques of ageing ungulates, yet no single method has yet been developed which can be used with any degree of accuracy beyond the first few years of age. The ageing of mature animals has proved to be extremely difficult in all studies so far carried out.

There are several techniques that have been attempted, some of which are more useful than others. The latest and most comprehensive review of mammalian age determination methods is that of Morris (1972), who summarised the various anatomical features that have been used as follows:

1.	Size increase	a) body mass
		b) linear dimensions
		c) baculum measurements
		d) eye lens mass
2.	Degradation	a) tooth wear
		b) loss of elasticity in collagen fibres
3.	Growth changes	a) tooth eruption and replacement
		b) bone marrow composition
		c) epiphyseal fusion
		d) external features, e.g. horns, antlers
4.	Incremental lines	a) tooth cement and dentine
		b) bone
		c) horns and claws

In addition to these certain special techniques are applicable to one or two groups of animals only.

8.2. Methods.

The mandibles of 1 145 impala which were shot in population control programmes in 1970, 1971, and 1972, were removed, labelled, dried, and stored for late examination. Both eyes of all animals from the 1970 and 1971 samples, as well as a few from the 1972 sample, were removed, slit, and preserved in 10% formalin.

The mandibles were examined as follows:

1. The state of eruption of the teeth was recorded.
2. In all jaws with complete dentition (and 16 with incomplete permanent dentition) the state of

wear on the molars, based on the classification of Vincent (1972), was recorded. Individuals were then allocated to wear classes in accordance with the criteria listed in Table 24. The various wear classes which are defined there are illustrated in Figure 18.

3. The wear surface on the first incisors was measured with a vernier caliper as shown in Figure 19, and described by Vincent et al (1968) and by Vincent (1972). The sum of the widths (lateral measurements) of the first incisors was divided by the sum of their lengths (measured anteroposteriorly), and this figure - the incisor index - was used as an index of age.

4. Approximately 150 specimens were selected for root sectioning in an attempt to count cementum annuli. For this purpose, the first incisor and first molar of each specimen were treated. Sections of the roots, approximately 0,5 mm to 1 mm thick, were sawn both longitudinally and across by means of a diamond blade used for geological work. These sections were glued to microscope slides and ground on a wheel to a thickness of approximately 20 microns. They were then stained in Ehrlich's haematoxylon for 10 to 15 minutes, and rinsed under a tap before being dried and examined by reflected, incident and polarised light under a microscope.
A few teeth were simply sawn, and the faces polished with fine carborundum paste or paper and examined by incident light.

Table 24. Definitions of the adult tooth wear classes used for impala in Mkuzi Game Reserve.

WEAR CLASS	CODE	DEFINITION
Nil	Nil	No cusps worn smooth.
Light	L	Anterior cusp of M_1 worn smooth.
Light/Moderate	L/M	Posterior cusp of M_1 worn smooth.
Moderate	M	Posterior cusp of M_3 worn smooth.
Moderate/Heavy	M/H	Anterior cusp of M_2 worn smooth.
Heavy	H	Posterior cusp of M_2 worn smooth.
Very heavy	V.H.	Anterior cusp of M_3 worn smooth on one side only.
Extra heavy	E.H.	Anterior cusp of M_3 worn smooth on both sides.
Extra heavy plus	E.H.+	Middle cusp of M_3 worn smooth on one or both sides.

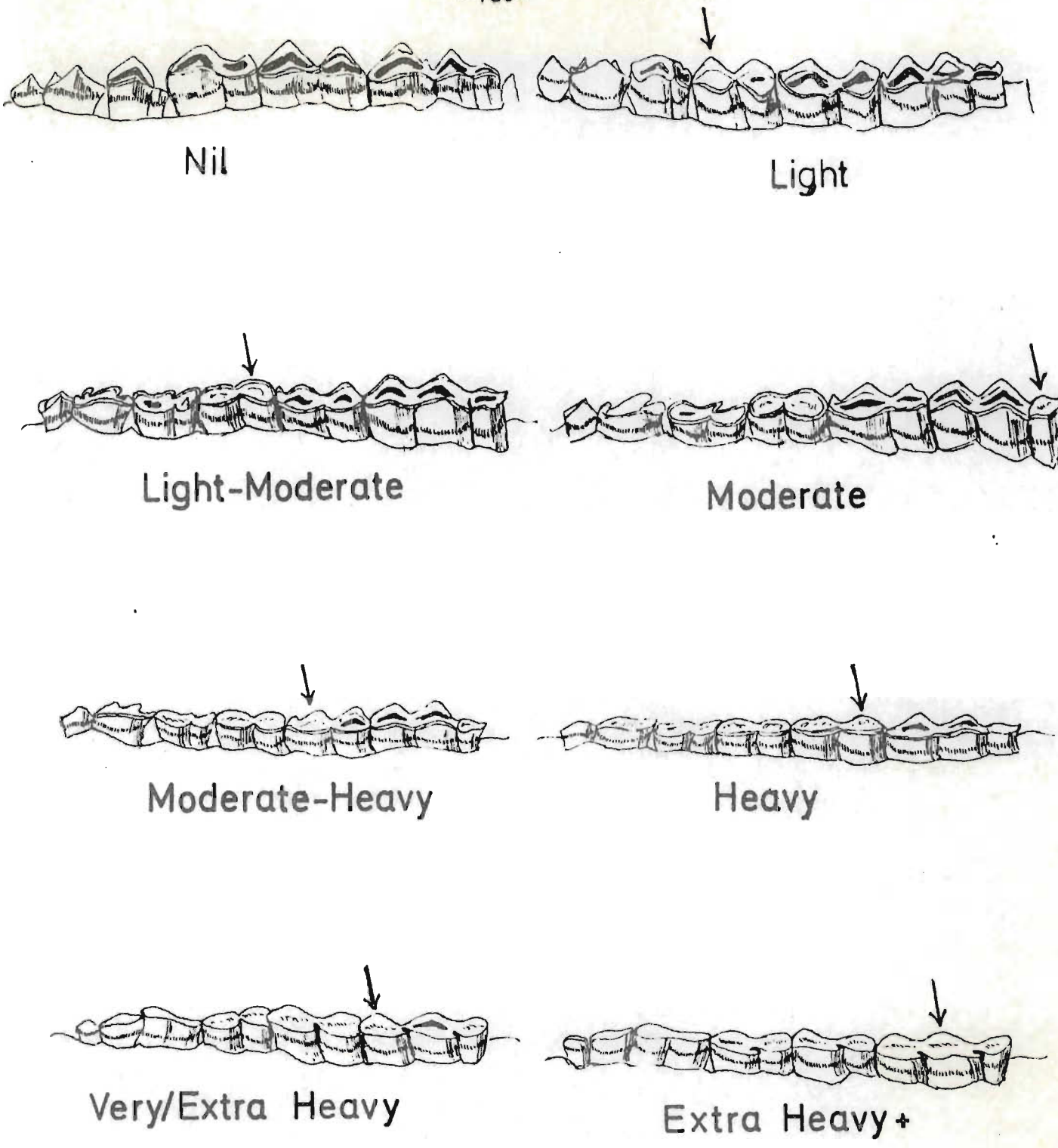

Figure 18. Sketches of the tooth rows of the various wear classes of impala. The arrow points in each case to that cusp which is the key to each class definition.

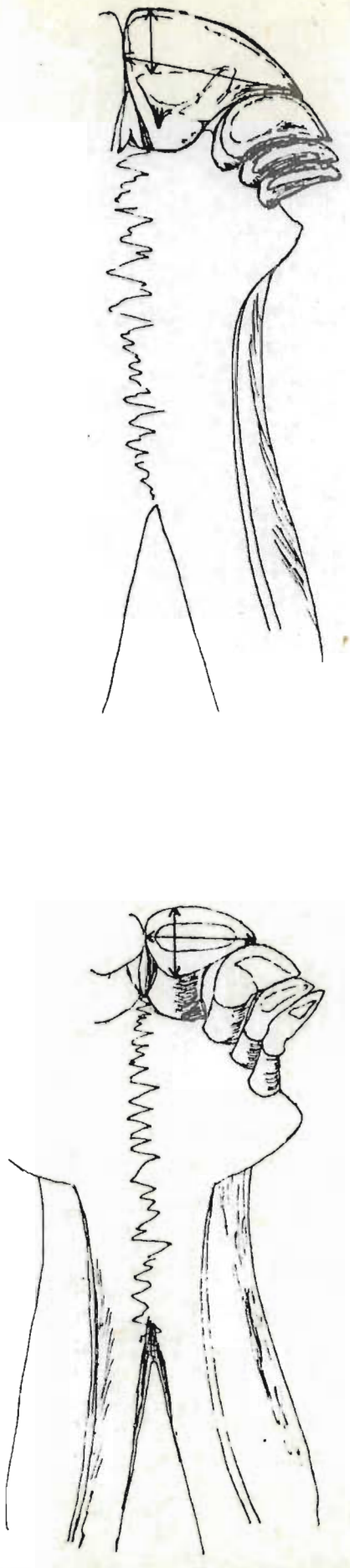

Figure 19. Sketches of the incisiform teeth of young (upper) and old (lower) impala, showing the conformation of the teeth and the method of measuring the "area" of wear - the incisor index.

5. The crown height of the first right mandibular molar of a total of 512 animals (498 with full permanent dentition and 14 with incomplete dentition), was measured to the nearest 0,1 mm with a vernier caliper. Figure 20 shows the method of measurement, from the "saddle" between the roots to the point midway between the two cusps on the buccal side.
6. The eye lenses, numbering 767 pairs, were removed from the eyeballs as soon as possible after collection and stored in 10% formalin solution for periods which varied from six months to two years. They were then dried in batches in an oven set at 85 - 90 ^{o}C until constant mass was attained. This was after about three days, when changes of mass between successive weighings of the same pairs varied by between 0,1% and 0,4%.
   In a sample of 100 pairs of lenses, the mass was determined before drying by removing excess moisture with blotting paper. The diameter (the mean of two measurements taken at right angles to each other) and the thickness of these lenses were measured with a vernier caliper in an effort to obtain a "density index".

A small sample of horns was examined for horn growth checks by sandpapering the bases of the horns, in order simply to remove the rough outside layer and to reveal the lower layers outside the bony core.

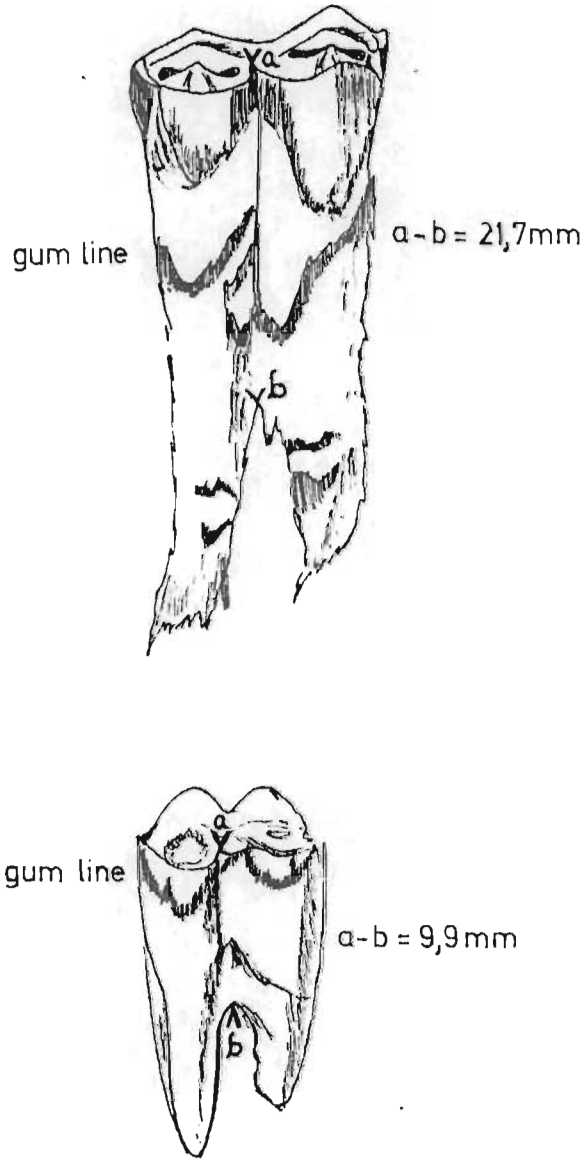

Figure 20. First molars of young (upper) and old (lower) impala, showing the method of measuring the height of the tooth for ageing purposes.

Finally, the total body mass of shot impala was recorded whenever possible.

8.3. Results.

8.3.1. Tooth eruption and replacement.

The normal tooth formula for impala is $I\frac{0}{3}$, $C\frac{0}{1}$, $Pm\frac{3}{2/3}$, $M\frac{3}{3}$. This agrees with that given by Child (1964) except that he recorded a full compliment of three premolars in the mandible. Of the sample of 848 animals with full permanent dentition examined from Mkuzi, 53 (6,3%) had the left lower Pm 2 missing, 41 (4,8%) had the right, and 117 (13,8%) had both missing. The difference between the left and right sides is not significant, although the number missing from the left was consistently more in each of the three yearly samples.

In a series of papers on abnormal dentition of impala from Rhodesia, a similar abnormality was reported in a small proportion of animals. Child and Riney (1964) found one mandible in a sample of 292 specimens with the second premolar missing in each ramus. Child (1965) found a further seven with this abnormality in a sample of 463 jaws - six with both second premolars missing and one with this tooth missing from the right ramus only. These two samples came from the same population in Rhodesia and the percentage with abnormalities was only 1,1%. In a further sample from another area in Rhodesia, Child (1969) reported a further two animals in a sample of 113 skulls with full permanent dentition (1,8%) with the right second premolar missing in the mandible. Thus the overall proportion of animals from Rhodesia with

abnormal dentition was 10/868 (1,15%), which compares with 211/848 (24,9%) from the Mkuzi population.

The trend, discussed by Child (1969), towards the progressive loss of anterior cheek teeth in certain ungulates is therefore very much more advanced in the Mkuzi population than it is in Rhodesia.

Child (1964) described the tooth eruption sequence of impala from populations in Rhodesia, supplementing his samples with a number of known-age specimens from the Transvaal. According to him, full permanent dentition is achieved at an age of about 29 months, the replacement of the premolars being the last stage in the sequence.

Grafton (1965) also used eruption as a means of ageing, and his results agree with those of Child (1964). Roettcher and Hofmann (1970) and Roettcher, Hofmann and Kayanja (1970) described the tooth eruption sequence in a population from East Africa, where the impala breed all year round, in contrast to populations studied previously. Where breeding is restricted to a short season it is necessary only to establish whether an animal is in its first, second or third year, whereas in East Africa it is necessary first to establish the eruption and replacement sequence before ages can be assigned. The only differences between the patterns described by Child (1964) and Roettcher et al (1970) are (i) the former indicated that the second mandibular molar is fully erupted by between 14 and 18 months, while the latter stated that it is erupted by 12 months, and (ii) the former found that the incisiform teeth are replaced between 17 and 22 months, while the latter gave

the period as 15 to 25 months. These minor differences may be due either to genetic differences between the two widely separated populations or to sampling inadequacies.

Vincent (1972) provided a chart showing the sequence of tooth eruption and replacement in impala in Mkuzi Game Reserve where breeding is seasonal. This differed from the findings of Child (1964) and Roettcher et al (1970) in the following important points:

a. The incisiform teeth are replaced in sequence from front to back, not simultaneously as reported by Child (1964).

b. Replacement of the premolars takes place between 22 and 28 months.

c. The third molar is still erupting at 32 months in some animals, although it may start erupting at 16 months.

In the present study, a larger sample (n = 297) was used, and a few minor modifications were made to the chart, which is shown in its modified form in Figure 21.

Caughley (1965), working on a population of Himalayan tahr Hemitragus jemlahicus in New Zealand, calculated the variability of the eruption time of each of the permanent mandibular teeth, instead of expressing the eruption sequence simply as the observed range. In doing so he challenged other authors to do the same for other ungulates. His method was used to calculate the variability for the Mkuzi impala population.

The median date of birth cannot be determined definitely,

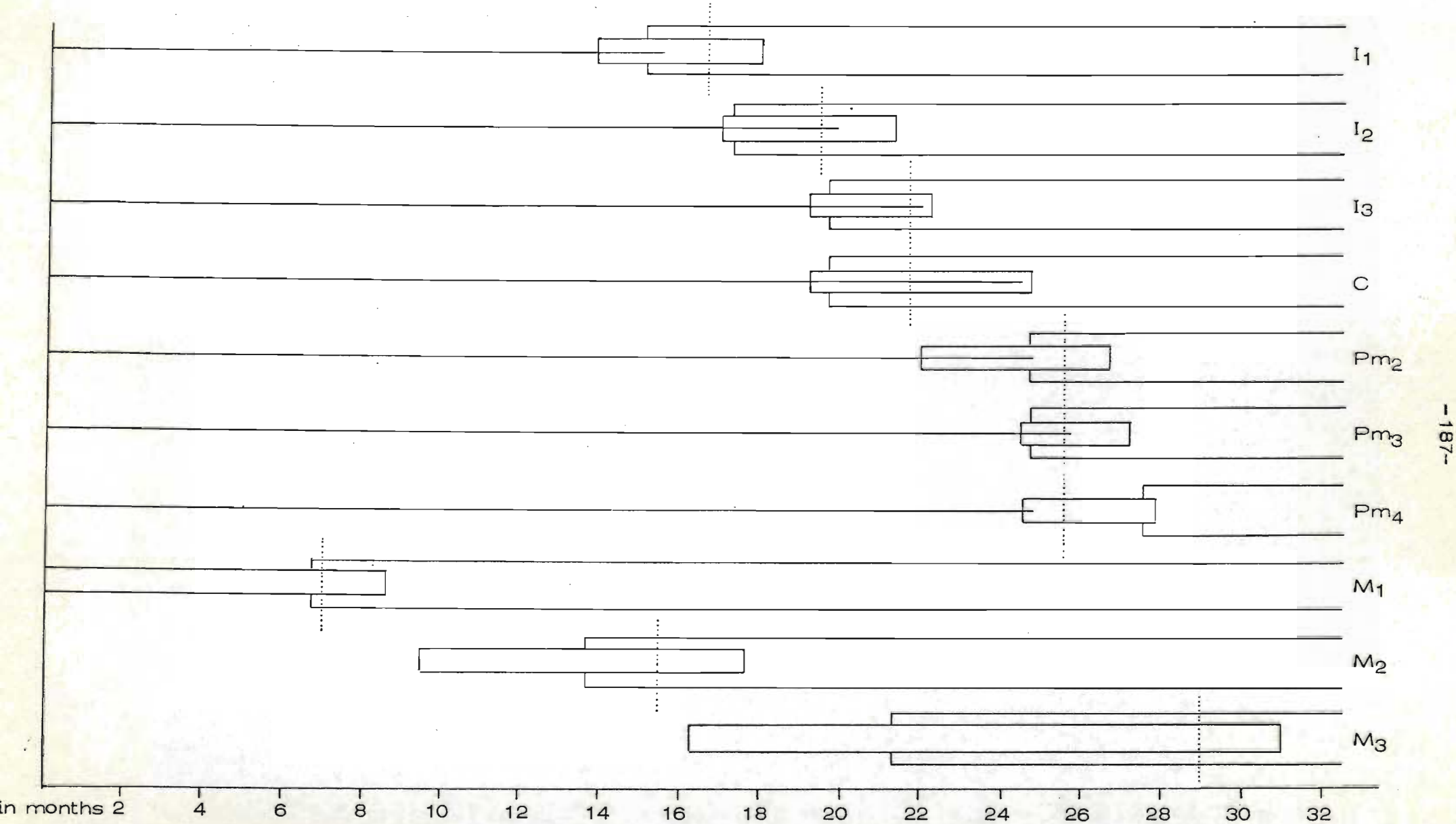

Figure 21. Tooth eruption and replacement chart for Mkuzi impala. A single line represents a deciduous tooth, a narrow bar an erupting or replacing permanent tooth, and a broad bar a permanent tooth that is fully erupted. Vertical dotted lines indicate the mean ages of eruption of permanent teeth. Data from a sample of 639 specimens.

but evidence from observations and records indicate that it is very close to 1 December each year. The spread of births can similarly not be accurately determined, but it seems very likely that it is about a week either side of the median date, with very few births occurring beyond that.

The cumulative percentages of animals in the sample which had reached or passed each stage of the eruption sequence in full are plotted in Figure 22 as a normal probability scale against age in months. The mean age of eruption of each tooth, together with its standard deviation and the age interval in which 95% of eruptions occur, is shown in Table 25.

8.3.2. Molar wear patterns.

Molar wear patterns have been estensively used as a means of ageing many species of ungulates. This technique is particularly valuable in the field, for it is rapid and simple. However, there are limitations which have been recognised both abroad (Robinette et al, 1957), and in Africa, where doubt has generally been more tacitly expressed. For instance, while he found some degree of correlation, Simpson (1974) was able to show, by comparing wear classes with cementum annuli counts in bushbuck Tragelaphus scriptus, that one wear class embraced more than one age class. Earlier, by the same means, Simpson and Elder (1969) had found a very close relationship between molar wear classes and the number of cementum annuli.

Roettcher and Hofmann (1970) and Roettcher, Hofmann and Kayanja (1970) assigned ages to a sample of impala jaws

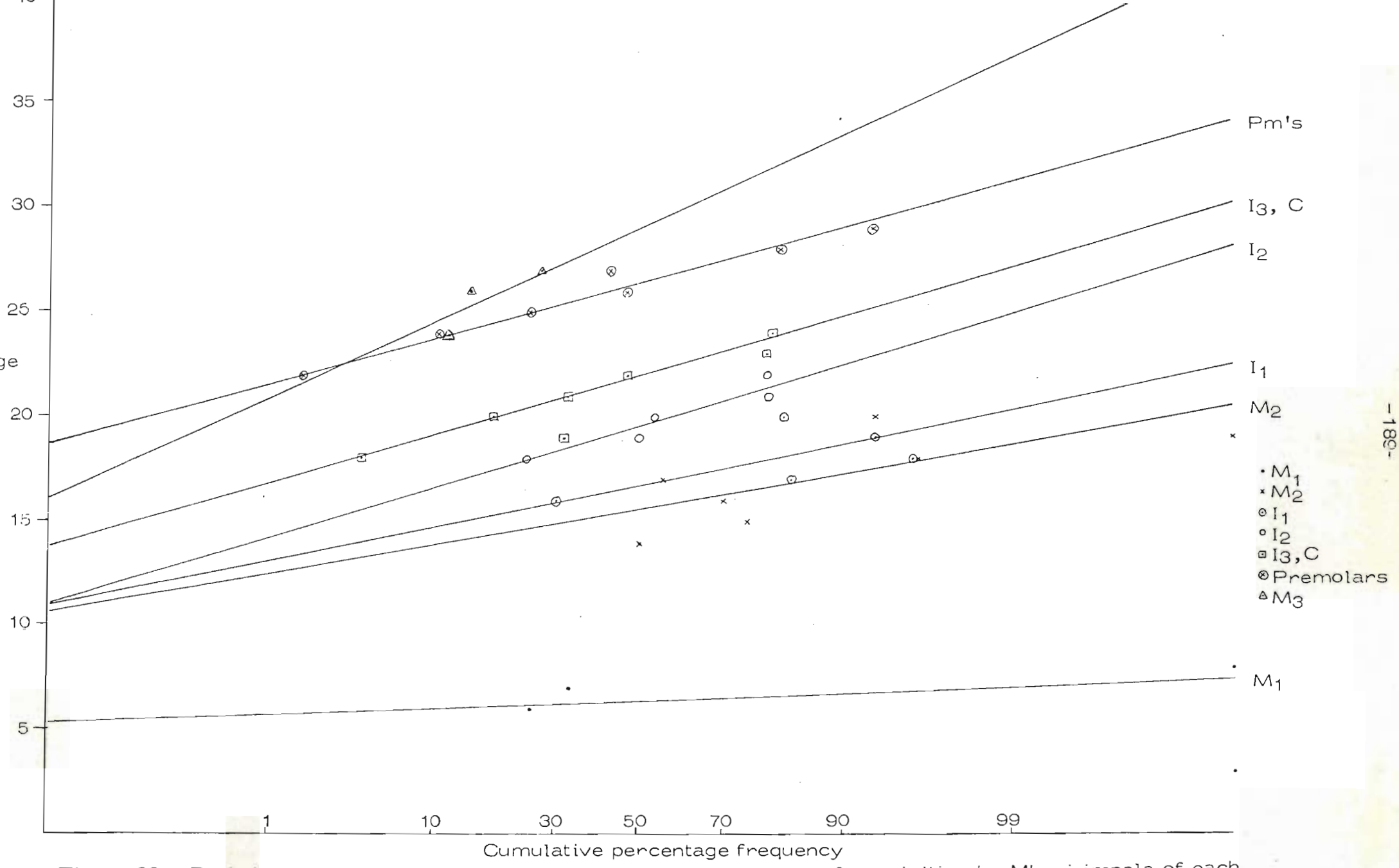

Figure 22. Probability paper plot of cumulative percentage frequency of acquisition by Mkuzi impala of each permanent tooth against age in months.

Table 25. Mean ages of eruption of permanent mandibular teeth of Mkuzi impala and their respective standard deviations from the mean, and the age intervals in which 95% of eruptions are completed.

Tooth	Mean age of eruption (months)	Standard deviation (months)	Age interval for 95% of eruptions (months)
M_1	6,5	0,27	6,0 - 7,0
M_2	15,5	1,34	12,8 - 18,2
I_1	16,75	1,55	13,7 - 19,9
I_2	19,5	2,28	14,9 - 24,1
I_3,C	21,75	2,28	17,2 - 26,3
Pm's	26,5	2,02	22,5 - 30,5
M_3	29,0	3,49	22,0 - 36,0

from an East African impala population on the basis of the wear patterns on the upper and lower molars. Their interpretation of ages was purely subjective, although they estimated that the accuracy of their determinations was to within $\pm$ 6 months up to eight years and $\pm$ 12 - 24 months after that. The nature of the attrition of the incisors and molars is described for each year class by these authors.

Spinage (1971) who, when he prepared his analysis, did not have the results of Roettcher et al available, used the same basis for ageing, and his results differed only slightly from those of Roettcher et al (1970).

Spinage (1971) derived a formula for the estimation of age based on the crown height of the first molar in both maxilla and mandible. The crown height was determined in the same way as has been described in this study, so that the results are comparable. It was assumed by Spinage (1971) that the height of the tooth in the absence of wear was 33 mm, and the age at which it is zero was 10 years, in order for the data to fit the formula. However, due to the fact that wear on the cheek teeth slows down with age because a greater overall grinding surface is presented, the regression of crown height on age is attenuated at advanced ages, and Spinage (1971) concluded that the mean life of the teeth is 12 years. The formula used is $y = y_0 (1 - (^t/n)^{1/2})$, where y is the crown height at time t, n is the age in years at which y is zero, and y_0 is the crown height before any wear occurs. Using Spinage's derived data, this becomes $y = 33 (1 - (^t/10)^{1/2})$ for M_1.

Spinage's (1971) method has merit when known-age

specimens are not available, for the application of his "conceptual wear model" enables ages to be derived when only extreme parameters are known. The formula he used depends on the assumption that marked variations in wear are random. In a population with an unrestricted breeding season the method is useful only on a population basis, but in one with a limited season such as in Mkuzi, it is to be expected that the differences of one year between successive age class groups will readily be detectable at any given time, and that the precise ages of individuals can therefore be determined.

Jarman (unpubl. ms.), in Cowley (1975), also used tooth eruption and attrition as a means of ageing impala in a population in Rhodesia. He divided eruption and wear of mandibular teeth into 18 classes, to which he allocated ages. The first nine classes, up to 24 months old, were based on eruption.

In the Mkuzi study, wear on the molars only was used to derive a series of classes, and the numbers of animals collected and allocated each month to each of these classes, as defined in Table 24, are shown in Table 26, together with the comparable wear or age classes derived by other authors. The distribution is illustrated in Figure 23. The comparisons in Table 26 are confused by the apparent important difference between the East African (Roettcher et al 1970, Spinage 1971) and Rhodesian (Cowley 1975) populations on the one hand, and the Mkuzi population. This takes the form of a difference in the order of wear on the molar cusps: in the former populations the third cusp of M3 is worn smooth only after the cusps of M_2 are smooth, whereas in Mkuzi impala this

Table 26. The number of impala collected each month in Mkuzi Game Reserve which were assigned to each of the tooth wear classes, and the corresponding ages allocated to these by other authors.

Class / Month	Nil	L	L/M	M	M/H	H	V.H.	E.H.	E.H.+	Total
January	2	1	8	2	1	1	0	0	1	16
February	6	15	19	6	4	2	0	1	3	56
March	7	12	10	3	2	3	1	2	4	44
April	8	3	11	6	2	1	1	1	2	36
May	33	30	45	7	7	7	3	4	4	140
June	9	21	18	5	4	3	2	4	2	68
July	7	20	16	2	2	4	0	3	3	57
August	16	32	34	6	1	2	0	4	6	101
September	26	58	72	11	11	14	2	7	9	210
October	7	22	21	4	2	4	0	1	3	64
November	3	8	9	1	4	2	0	1	2	30
December	2	10	15	5	1	3	1	3	2	42
Total	126	232	278	58	41	46	10	32	41	864
Roettcher et al (1970)	3y.	4y.	5y.		6y.		10–12y.			
Spinage (1971)	A	B	C	D	E	F	G	G		
Jarman (in Cowley (1975)	2–4y.	4–5y.	5–6y.		6–7y	7–10y	10–12y	12y+		

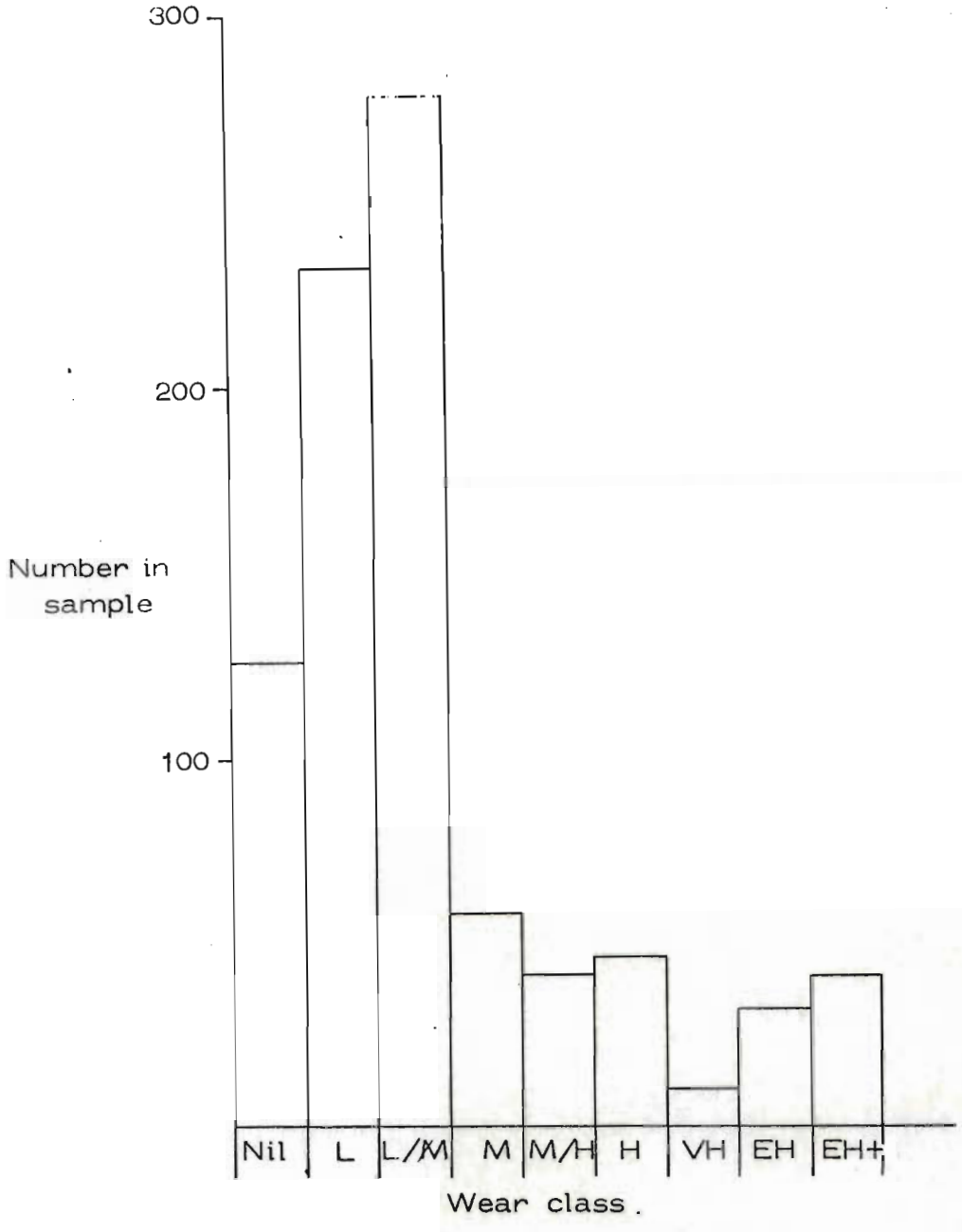

Figure 23. The frequency distribution of impala from Mkuzi Game Reserve which were allocated to each of the tooth wear classes.

occurs before M_2 is worn smooth.

The number of animals allocated to the light and light/moderate wear classes appears to be disproportionately high, and in fact 59% of the total sample is composed of animals in these two wear classes. It is possible therefore that they are made up of more than one year class each. For this reason, other methods of separating age classes were used.

Cowley (1975) comes to the same conclusion, namely that the number of animals in his 4 - 5 and 5 - 6 year old classes is high in relation to the 2 - 4 year classes, as aged by Jarman (unpubl. ms.). He attributed this to rapid initial wear on M_1, as described by Spinage (1971), and states that young animals appear older than they really are. This applies equally to the Mkuzi population, although it is suspected that the Light and Light/Moderate wear classes also contain a number of animals older than may be assumed by allocating ages on an eclectic basis.

8.3.3. Incisor index.

Roettcher et al (1970) used a subjective assessment of the wear on the crown enamel of the first incisor, in conjunction with molar wear, as a means of age determination, and in the 7 - 9 year age groups restricted their examination of wear exclusively to I_1. They based their allocation to age groups on the successive attrition of the incisiform teeth, and on the size of the area of wear on each.

The mean incisor index (See 8.2.(3)) for each of the

established wear classes is shown in Table 27. From this it is clear that the value of the index decreases with age, if it is assumed that the succession of molar wear classes represents increasing age. The values are illustrated in Figure 24.

It is not possible in this analysis to assign definite ages to the incisor index values in the absence of known-age specimens. The coefficient of variation of the value in each wear class was too large to justify the examination of any form of correlation between incisor index and wear class.

The values of the incisor index were then analysed on their own. Two sub-samples were extracted from the total sample, these being composed of 169 specimens obtained in May and 319 in August/September, representing 17,0% and 31,5% of the sample respectively.

A basic premise in the further analysis assumes the seasonal nature of births in the population being studied, and that this season is the same each year. This has already been established. This being the case, it is to be expected that a sample taken at any one time will contain animals whose ages differ by exactly one year. A sample taken over a period of one or two months should not vary sufficiently to create undue overlap in the values of the parameter being studied between successive year classes. A frequency distribution of these values should therefore be polymodal.

Harding (1949) devised a method of analysing polymodal

Table 27. The mean incisor index for each wear class of Mkuzi impala for the whole year, with standard error of the means, standard deviation, and coefficient of variation (C.V.) of the samples.

Class	No. in sample	Mean ± S.E.	Standard deviation	C.V.
Yearling	68	9,868 ± 0,714	5,887	59,7
Two-year	92	6,975 ± 0,150	1,439	20,6
Nil	117	5,658 ± 0,099	1,070	18,9
Light	227	4,891 ± 0,081	1,223	25,0
Light/Moderate	271	3,353 ± 0,027	0,437	13,0
Moderate	58	2,812 ± 0,114	0,869	30,9
Moderate/Heavy	37	2,389 ± 0,082	0,496	20,8
Heavy	46	1,914 ± 0,104	9,705	36,8
Very heavy	10	1,818 ± 0,158	0,500	27,5
Extra heavy	32	1,621 ± 0,074	0,418	25,8
Extra heavy plus	34	1,468 ± 0,075	0,436	29,7

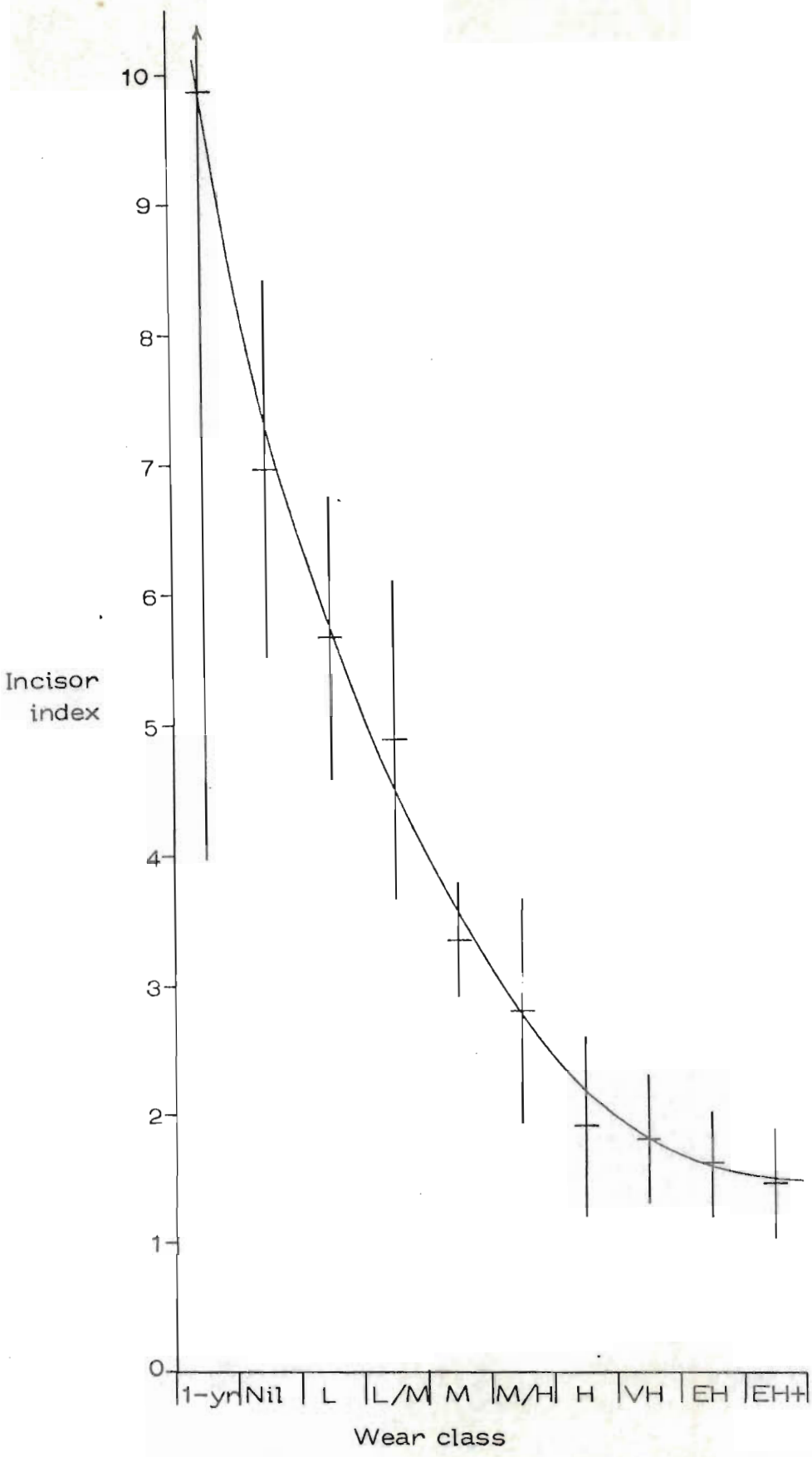

Figure 24. Incisor index values plotted against molar wear classes of impala in Mkuzi.

frequency distributions, using probability graph paper. This paper is described as having a scale of percentages along the bottom, reading from 0,01% on the left to 99,99% on the right. The scale is more crowded towards the middle than on the ends, and is so arranged that when a normal distribution is plotted, the points fall in a straight line instead of in a parabola. The method of plotting described by Harding (1949) requires a certain amount of trial and error to determine the position of the normal distribution.

Cassie (1954) modified the method of plotting to eliminate most of the trial and error in Harding's method, and it is this modified and simplified method which is used in this study. The method used to extract the respective distributions is explained in Appendix 1.

The incisor index is recorded to the first decimal place and, because of the comparatively small sample sizes the values are grouped in intervals of 0,2. From ageing by tooth eruption it is known that most specimens with an index of about 5,0 or greater belong to animals less than three years of age. There is therefore a wide spread in the value of the incisor index of this age class - from about 5,0 to 8,0 and more - because of the rapid initial attrition of the wear area on the first incisor.

The frequency, cumulative frequency, and cumulative percentage frequency distributions of the incisor index in the two sub-samples are shown in Table 28. The plots on probability paper of these percentage frequencies are shown in Figures 25 and 26, together with the extracted normal

Table 28. The frequency (f), cumulative frequency (F), and cumulative percentage frequency (%) of incisor index values at intervals of 0,2 of two samples of impala from Mkuzi. 1970 and 1971 samples combined.

Interval	May sample			September sample		
	f	F	%	f	F	%
0,8 - 1,0				3	3	1,0
1,0 - 1,2	2	2	1,2	3	6	1,9
1,2 - 1,4	1	3	1,8	4	10	3,2
1,4 - 1,6	6	9	5,3	15	25	7,9
1,6 - 1,8	5	14	8,3	15	40	12,7
1,8 - 2,0	1	15	8,9	5	45	14,3
2,0 - 2,2	2	17	10,1	6	51	16,2
2,2 - 2,4	5	22	13,0	5	56	19,0
2,4 - 2,6	6	28	16,6	9	65	20,6
2,6 - 2,8	5	33	19,5	11	76	24,1
2,8 - 3,0	4	37	21,9	12	88	27,9
3,0 - 3,2	8	45	26,6	19	107	34,0
3,2 - 3,4	2	47	27,8	19	126	40,0
3,4 - 3,6	10	57	33,7	14	140	44,4
3,6 - 3,8	12	69	40,8	15	155	49,2
3,8 - 4,0	8	77	45,6	18	173	54,9
4,0 - 4,2	4	81	47,9	18	191	60,6
4,2 - 4,4	9	90	53,3	12	203	64,4
4,4 - 4,6	11	101	59,8	16	219	69,5
4,6 - 4,8	2	103	60,9	16	235	74,6
4,8 - 5,0	5	108	63,9	10	245	77,8
5,0 - 5,2	11	119	70,4	11	256	81,3
5,2 - 5,4	1	120	71,0	10	266	84,4
5,4 - 5,6	10	130	76,9	7	273	86,7
5,6 - 5,8	6	136	80,5	3	280	87,6
5,8 - 6,0	5	141	83,4	1	281	87,9
6,0 +	28	169	100,0	38	319	100,0

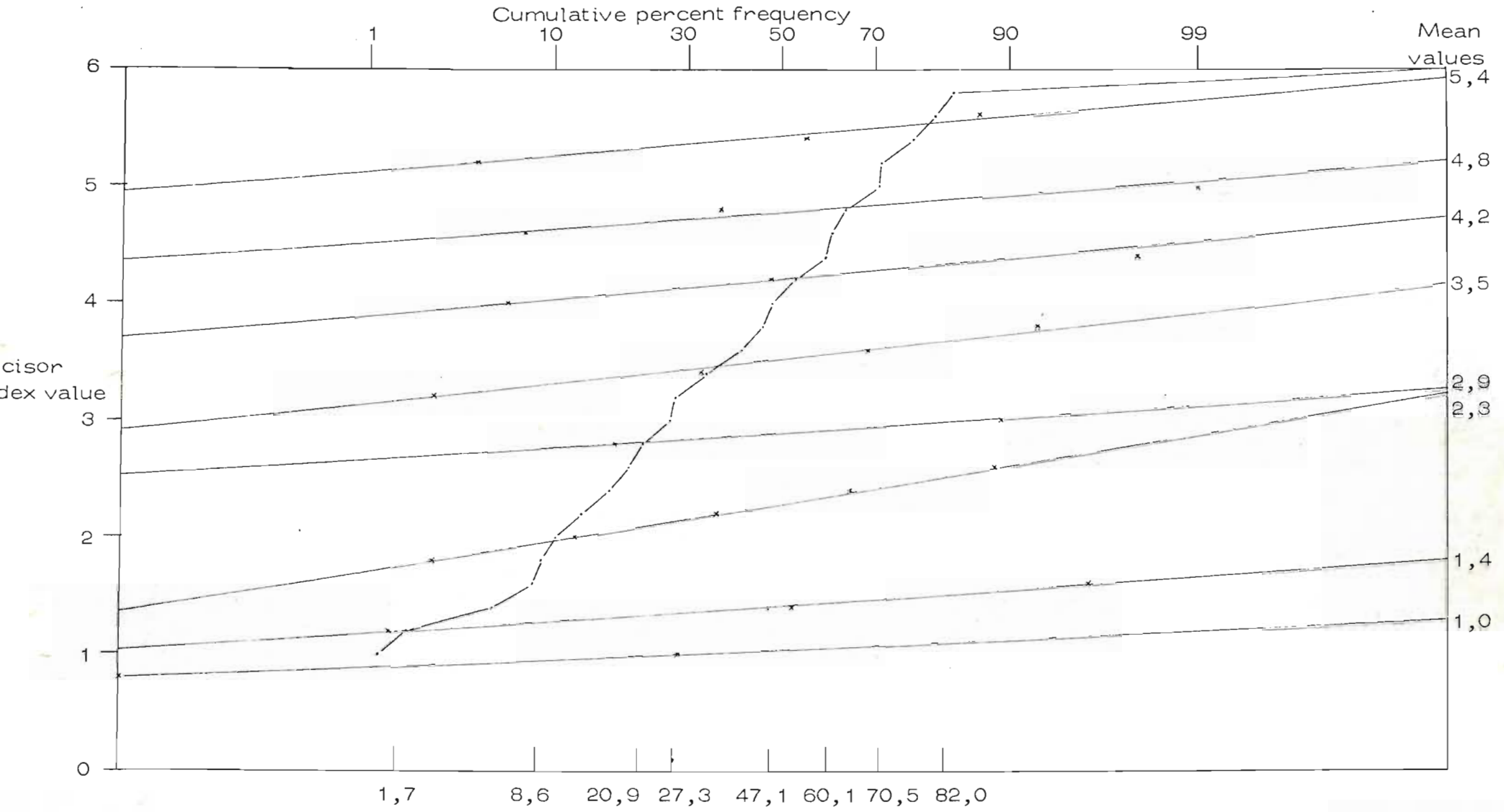

Figure 25. Probability paper plot of cumulative percentage frequency of incisor index values in class intervals of 0,2 for the May sample of 169 Mkuzi impala (dots) and the extracted normal distributions (crosses).

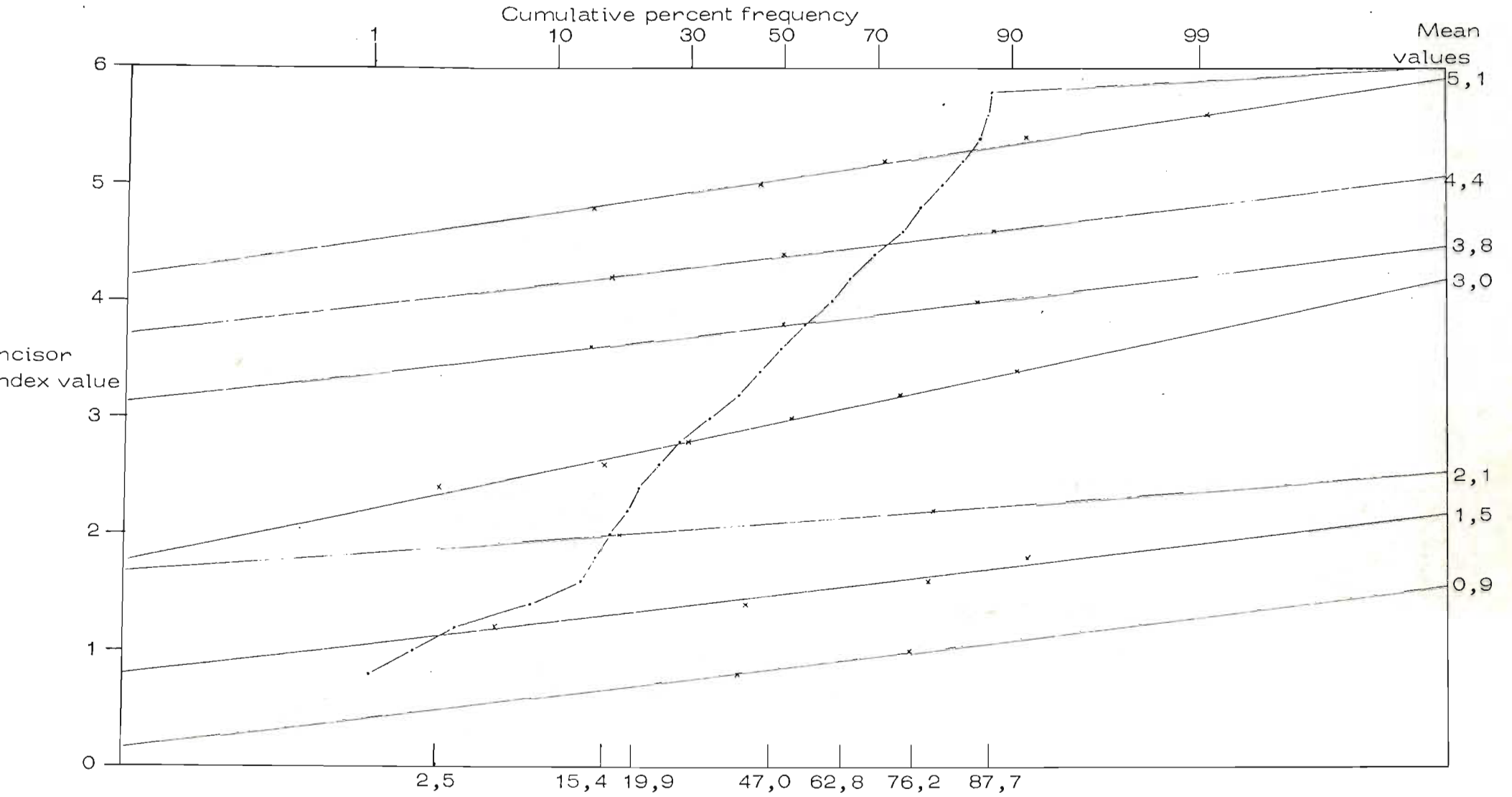

Figure 26. Probability paper plot of cumulative percentage frequency of incisor index values in class intervals of 0,2 for the August/September sample of 319 Mkuzi impala (dots) and the extracted normal distributions (crosses).

distributions, which are seen as straight lines superimposed on the frequency distribution. The results of the analyses are shown in Table 29.

Classes A and B in the analysis (Table 29), representing the oldest age classes, probably contain more than one age class each, because by this stage the wear area of I_1 is almost round and the tooth stub almost cylindrical. There is therefore little if any annual change in the wear area and therefore in the incisor index. Class I contains all the 2 - 3 year olds. There is one less class in the August/September sample than that in the May sample, and it is suspected that Class D in the August/September sample contains at least two age classes which cannot be separated by the graphical method. Both the calculated frequency in Class D and the large standard deviation support this probability.

The conclusion drawn from the analysis is that the method is not sensitive enough to reflect the limits, in small samples, of a parameter which is in any event subject to considerable variation. Nevertheless, it does enable separation of probable age classes to be achieved with some degree of success.

8.3.4. Cementum lines.

The ageing of African ungulates by means of annuli in the dental cementum has received a fair amount of attention. Temperate animals exhibit a fairly distinct annual pattern of cementum layers, but results on tropical African ungulates

Table 29. Analysis of data from the frequency distributions of two incisor index sub-samples of Mkuzi impala. $\bar{x}$ = mean value, s = standard deviation, n = calculated frequency.

Size class	May sample				August/September sample			
	$\bar{x}$	s	% of total	n	$\bar{x}$	s	% of total	n
A	1,0	0,3	1,7	2,9	0,9	0,6	2,5	8,0
B	1,4	0,4	6,9	11,7	1,5	0,7	12,9	41,2
C	2,3	0,9	12,3	20,8	2,1	0,4	4,5	14,4
D	2,9	0,4	6,4	10,8	3,0	1,2	27,1	86,4
E	3,5	0,6	19,8	33,5	3,8	0,7	15,8	50,4
F	4,2	0,5	13,0	22,0	4,4	0,7	13,4	42,7
G	4,8	0,4	10,4	17,6	5,1	0,8	11,5	36,7
H	5,4	0,5	11,5	19,4				
I			18,0	30,4			12,3	39,2

have been inconclusive. A source of some controversy has been the deposition in some areas of two layers per year and in others of only one, without any apparent correlation with climate. Klevezal and Kleinenberg (1967) reviewed the technique on a world wide basis, while Spinage (1976) has more recently reviewed it for African mammals. The latter draws attention to the difference between "double lines" caused by convolutions of the layers, and two lines being laid down per year. While the technique may be useful for temperate animals, its use for tropical mammals appears to be limited.

Grafton (1965) tried the dental cementum technique for ageing impala, but did not find any layers at all. Spinage (1971) was also unable to find any lines in over one hundred specimens examined.

In this study both the cement "boss" beneath M_1, favoured by Low and Cowan (1963) for deer, and by Simpson (1969) and Simpson and Elder (1969) for kudu, and the "pad" on I_1 used by Spinage (1967) in waterbuck Kobus defassa, were sectioned. A very few teeth showed vague lines, but they were so indistinct that it was not possible to count them.

As a means of ageing impala therefore, this technique would appear to be valueless, although more refined methods may help.

8.3.5. Crown height of first molar.

Molar height is of course related to the amount of wear borne by the tooth. The method of measuring crown height appears to have been used first by Spinage (1971) who measured it on M_1 in samples of two animals from each of his wear classes. A definite tendency towards reduction in this measurement with age is apparent from his results. On the basis of a formula derived from the observed maximum measurement and the theoretical age at which it becomes zero, ages of individuals were calculated, and these animals were allocated to each of the wear classes. The pattern of wear follows a negative exponential form, and Spinage (1971) explains this on the grounds that, as the opposing grinding surfaces become smoother, the friction between them decreases.

The formula derived by Spinage (1971) is $y = y_0 (1 - {}^{t}/_{n})^{1/2})$, in which y is the height of the tooth in year t, n is the year in which the height is assumed to be zero, and y_0 is the initial height of the tooth. He points out that this suggests that for each year of age, the height of the tooth is reduced by the square root of the preceding height (not the square as stated by Spinage). He used $y_0 = 33$ and $n = 14$ in his calculations, having based the age at which y is zero on records of longevity given by Skinner (1969) and Fairall (1969). He suggests that an average ecological maximum longevity for impala in the wild is about 9 years, give or take a year. In the absence of predators, it is suggested that this maximum is probably higher in Mkuzi.

In order to test the validity of the conceptual model proposed by Spinage (1971) the technique of Harding (1949) and of Cassie (1954) was used to separate year classes. The same premise as applies in relation to the incisor index, namely that births are strictly seasonal and take place at the same time each year, is also necessary for molar height analysis. This means that the measurements of the parameter should be grouped in age classes with intervals of one year. In order to fulfil this requirement, sub-samples of 85 specimens in May and 179 in August/ September, all with full permanent dentition, were examined. These represent 16,6% and 35,0% of the total sample respectively. The frequency distributions in class intervals of 0,4 mm are given in Table 30, and are represented graphically in Figures 27 and 28. The analyses are shown in Table 31.

If it is accepted that the extracted normal distributions each represent an age class, then Class K is probably composed of animals between 2 and 3 years old, and Class A of animals over 12 years old. The 2 - 3 year old class is poorly represented because many of the animals did not have full permanent dentition, and only a very few teeth from these were measured. The assumed ages of the various classes are included in Table 31. The reason for the assumption that the last class comprises 2 - 3 year olds is that some of the animals which had no molar wear actually had molar heights of about 15 mm, and these animals had clearly very recently achieved full permanent dentition.

From the standard deviations of mean molar heights

Table 30. The frequency (f), cumulative frequency (F) and percentage cumulative frequency (%) of first molar heights at class intervals of 0,4 mm, of two samples of impala from Mkuzi. 1970 and 1971 samples combined.

Class interval	May sample			August/September sample		
	f	F	%	f	F	%
2,0 - 2,3	0	0	0	1	1	0,4
2,4 - 2,7	1	1	1,2	1	2	0,7
2,8 - 3,1	0	1	1,2	0	2	0,7
3,2 - 3,5	0	1	1,2	1	3	1,1
3,6 - 3,9	0	1	1,2	3	6	2,2
4,0 - 4,3	1	2	2,4	1	7	2,6
4,4 - 4,7	1	3	3,5	6	13	4,8
4,8 - 5,1	0	3	3,5	2	15	5,0
5,2 - 5,5	3	6	7,1	9	24	8,9
5,6 - 5,9	1	7	8,2	6	30	11,2
6,0 - 6,3	2	9	10,6	4	33	12,3
6,4 - 6,7	3	12	14,1	3	36	13,4
6,8 - 7,1	1	13	15,3	10	46	17,1
7,2 - 7,5	3	16	18,8	6	52	19,3
7,6 - 7,9	1	17	20,0	4	56	20,8
8,0 - 8,3	2	19	22,4	3	59	21,9
8,4 - 8,7	4	23	27,1	8	67	24,9
8,8 - 9,1	2	25	29,4	11	78	29,0
9,2 - 9,5	5	30	35,3	11	89	33,1
9,6 - 9,9	4	34	40,0	15	104	38,7
10,0 - 10,3	2	36	42,4	7	111	41,3
10,4 - 10,7	4	40	47,1	17	128	47,6
10,8 - 11,1	5	45	52,9	14	142	52,8
11,2 - 11,5	2	47	55,3	7	149	55,4
11,6 - 11,9	3	50	58,8	20	169	62,8
12,0 - 12,3	4	54	63,5	15	184	68,4
12,4 - 12,7	5	59	69,4	3	187	69,5
12,8 - 13,1	1	60	70,6	6	193	71,7
13,2 - 13,5	1	61	71,8	15	208	77,3
13,6 - 13,9	5	66	77,6	18	226	84,0
14,0 - 14,3	8	74	87,1	15	241	89,6
14,4 - 14,7	4	78	91,8	6	247	91,8
14,8 - 15,1	2	80	94,1	3	250	92,9
15,2 - 15,5	1	81	95,3	6	256	95,2
15,6 - 15,9	2	83	97,6	9	265	98,5
16,0 - 16,3	2	85	100,0	3	268	99,6
16,4 +				1	269	100,0

August 87
September 182

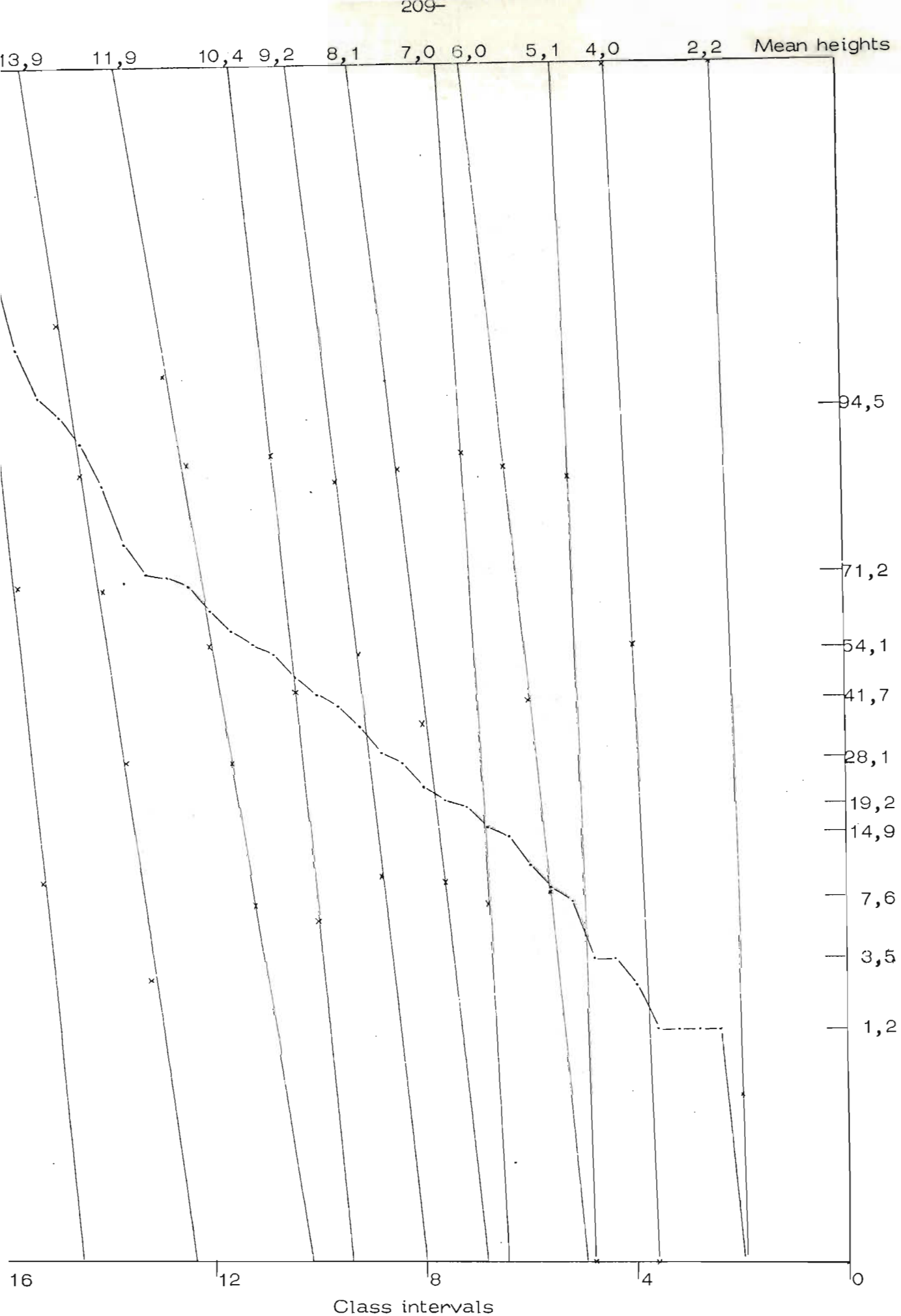

Figure 27. Probability paper plot of cumulative percentage frequency of first molar heights at class intervals of 0,4 mm for the May sample of 85 Mkuzi impala (dots) and the distributions of the inferred age classes (crosses).

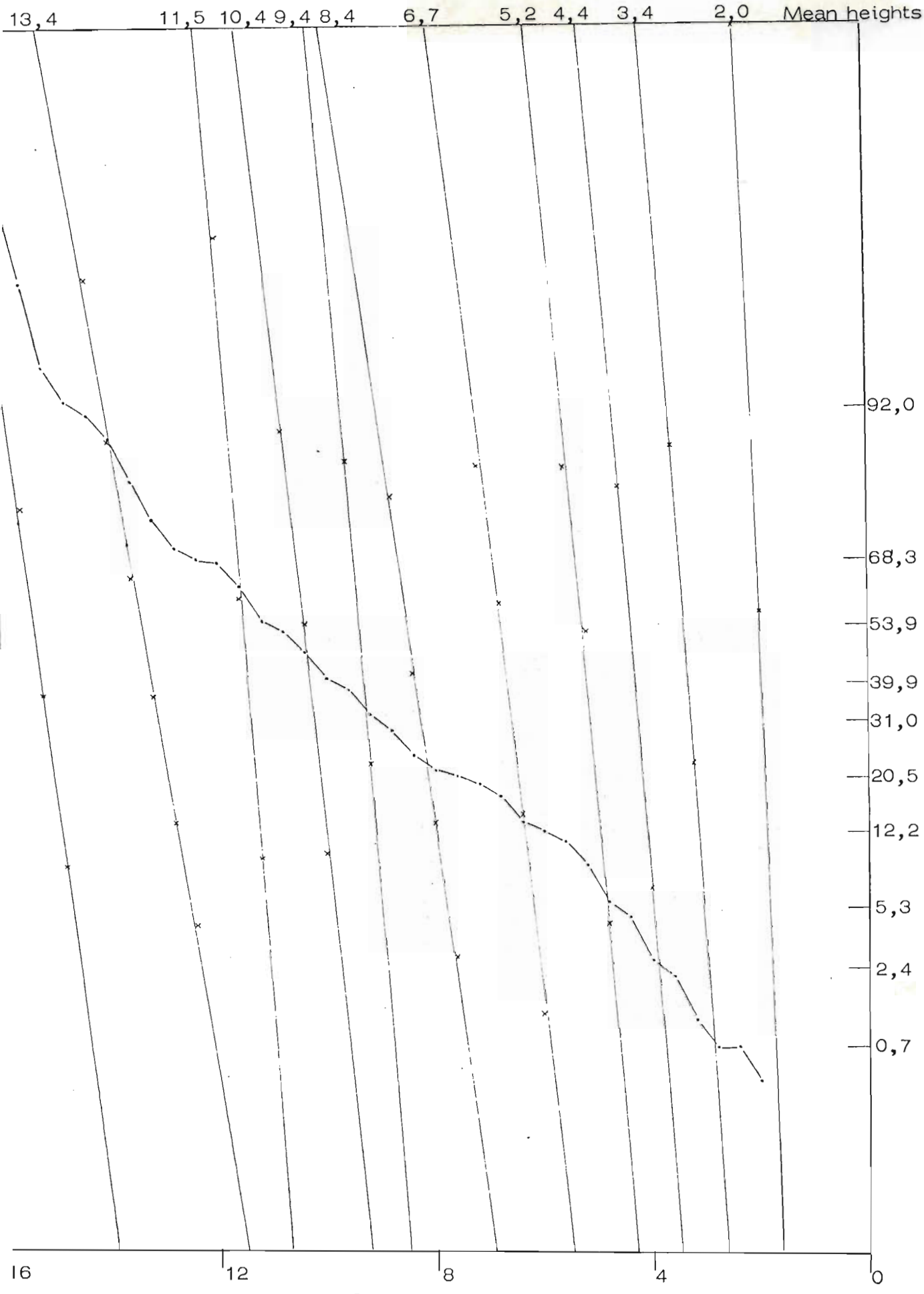

Figure 28. Probability paper plot of cumulative percentage frequency of first molar heights at class intervals of 0,4 mm for the August/September sample of 269 Mkuzi impala (dots) and the distributions of the inferred age classes (crosses).

Table 31. Analysis of data from the frequency distributions of two samples of first molar heights of Mkuzi impala. $\bar{x}$ = mean height (in mm), s = standard deviation, n = calculated frequency.

Class	Age (years)	May sample				August/September sample			
		$\bar{x}$	s	% of total	n	$\bar{x}$	s	% of total	n
A	12 +	2,2	0,7	1,2	1,0	2,0	2,2	0,7	1,9
B	11 - 12	4,0	1,5	2,3	2,0	3,4	2,6	1,7	4,6
C	10 - 11	5,1	1,1	4,1	3,5	4,4	3,0	2,9	7,8
D	9 - 10	6,0	4,5	7,3	6,2	5,2	3,7	6,9	18,6
E	8 - 9	7,0	2,6	4,3	3,7	6,7	4,8	8,3	22,3
F	7 - 8	8,1	4,5	8,9	7,6	8,4	6,0	10,5	28,2
G	6 - 7	9,2	4,5	13,6	11,6	9,4	3,0	8,9	23,9
H	5 - 6	10,4	3,7	12,4	10,5	10,4	4,1	14,0	37,7
I	4 - 5	11,9	6,3	17,1	14,5	11,5	3,0	14,4	38,7
J	3 - 4	13,9	6,0	23,3	19,8	13,4	6,7	23,7	63,8
K	2 - 3	15,5	4,1	5,5	4,7	15,3	6,0	8,0	21,5

in each class it can be seen that, with very few exceptions, and given the molar height, it should be possible to age individuals to within one year. As has been stated by Spinage (1971) a variation of this magnitude is unlikely to affect general interpretations of population dynamics. The important consideration is that the method described here would appear to be the most efficient devised to date for impala.

It is now possible to test Spinage's (1971) hypothesis that the height of the tooth is reduced each year by the square root of the preceding year's height. The data obtained from Mkuzi do not support the hypothesis at all, as the factor by which the height is reduced varies by between 0,9 root and 1,4 root. In other words the rate of wear is not consistent. The maximum potential height at age 0, given by Spinage (1971) as 33 mm, is academic, because between 0 and about 7 months, M_1, is in a stage of rapid growth.

The height of the first molar plotted against the derived ages is shown separately for the two samples obtained in May and in August/September respectively, in Figures 29 and 30. The curves have been drawn by eye, and are remarkably similar in form. Molar height values for six individuals with teeth in various stages of eruption are shown as crosses in Figures 29 and 30. The curves cannot satisfactorily be fitted to these points because of the wide variation in rate of wear at this stage.

The conclusion to be drawn from the data is that wear on

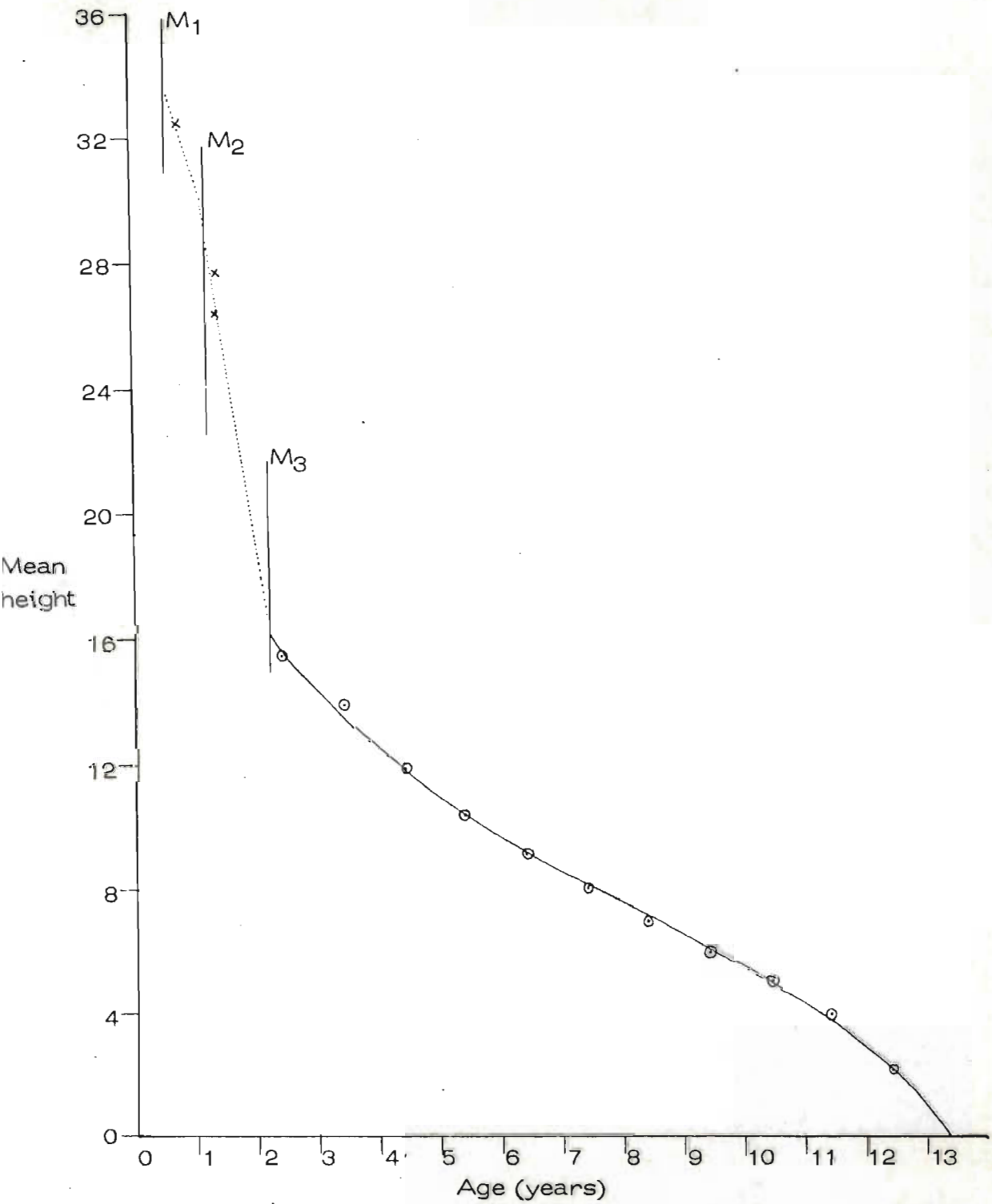

Figure 29. Height of first molar in mm plotted against age derived by the probability paper method. Vertical lines indicate mean ages at which the molars are fully erupted, and crosses indicate the heights of individual first molars at ages of less than 2,25 years. May sample.

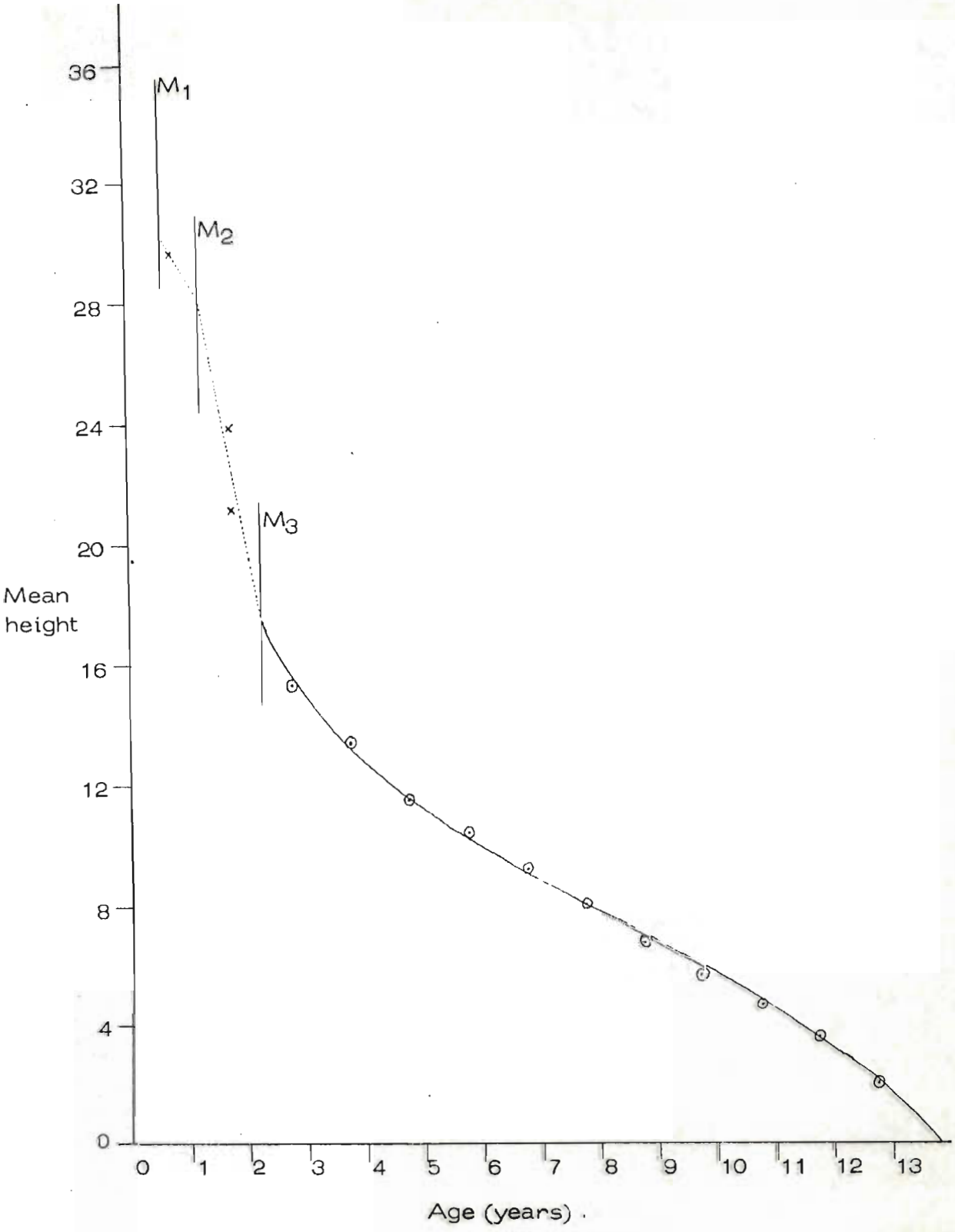

Figure 30. Height of first molar in mm plotted against age derived by the probability paper method. Notation as in Figure 29. August/September sample.

the first molar is extremely rapid during the first two years of life. This agrees with the finding of Spinage (1971) who explains this by pointing out that M_1 takes the brunt of the wear until M_2 and M_3 enter the "arc of attrition". It will be seen from Table 25 that M_2 is fully erupted on average at 15 months (1,25 years) and M_3 at 27 months (2,25 years). M_1 is fully erupted at only 7,25 months (0,6 year). These events have been drawn into Figures 29 and 30 as vertical lines, and the theoretical wear extrapolated with dotted lines so as best to fit the values between the eruptions of M_2 and M_3. The maximum height of M_1, by extrapolation, is calculated as 33,8 mm from the May sample, and 30,2 mm from the August/September sample.

At the other end of the graph, the age at which the height of M_1 reaches the theoretical height of zero is read off as 13,3 and 13,8 years from the respective samples. However, this value is probably never achieved in fact, and the lowest height recorded of 2,1 mm is probably about as far as it is likely to go before the process of chewing becomes impossible. In other words, the maximum longevity is about 12,5 years under the conditions imposed on impala by the Mkuzi environment.

The mean range of molar height for each age class, can be read off from the curves in Figures 29 and 30, and is shown in Table 32. The mean values at the beginning and end of each age class may be read off from the two graphs. In this way it is possible to age all animals in the sample with reasonable accuracy.

Table 32. Range of height of first molar in each age class of Mkuzi impala.

Age	Mean height at start of year class (mm)	Mean height at end of year class (mm)
2 - 3	19,7	14,7
3 - 4	14,7	12,65
4 - 5	12,65	11,1
5 - 6	11,1	9,8
6 - 7	9,8	8,7
7 - 8	8,7	7,65
8 - 9	7,65	6,5
9 - 10	6,5	5,55
10 - 11	5,55	4,4
11 - 12	4,4	3,0
12 +	3,0	(0)

Spinage (1971) discusses the effect of diet on tooth wear, and states that the rate of wear is unlikely to vary much genetically within a single species because of the importance of the teeth. It may however, vary within limits between populations on account of the nature of the diet. This would account for the longevity of an impala of at least 14 years recorded by Skinner (1969) from the northern Transvaal.

In order to test for sexual dimorphism in molar height, the August/September sample was treated separately for males and females by plotting the cumulative percentage frequency against the molar height and then analysing this plot. There were 42 males and 227 females in the sample, and the analysis is shown in Table 33.

In age classes D and H the mean molar height of females is slightly larger than that of males, in C and E it is the same in both sexes, and in the remaining six classes the males have a slightly larger mean size than females. None of the differences is significant. There remains only the unlikely possibility that one or the other sex has molars that are larger by the equivalent of the difference between age classes. It is therefore concluded that there is no sexual dimorphism in tooth size.

Using the information from Table 33, all the animals over two years of age in sample of 294 in 1970 and 218 in 1971 were aged and the distributions are shown in Table 34. From this it is quite clear that there was no significant difference between the age distributions in the two years of sampling: in no single age group was chi square higher than 0,08, and with a probability

Table 33. The mean molar heights of male and female impala, with standard deviations and calculated sample proportions and sizes of each age class.

Age class	Males				Females			
	$\bar{x}$	s	% of total	n	$\bar{x}$	s	% of total	n
A	2,0	2,2	1,8	1,9				
B	3,7	1,4	3,1	3,3	3,6	1,3	0,7	1,1
C					4,7	2,7	4,8	7,7
D	5,7	2,8	4,9	5,3	5,8	3,6	8,2	13,2
E	6,8	4,4	5,8	6,3	6,8	4,0	10,0	16,1
F	8,1	5,9	10,6	11,4	7,9	5,0	10,4	16,7
G	9,4	3,1	3,8	4,1	9,1	2,2	12,2	19,6
H	10,3	3,8	15,6	16,8	10,4	4,2	12,9	20,8
I	11,7	2,8	15,4	16,6	11,4	2,6	13,7	22,1
J	13,4	6,4	35,7	38,6	13,3	5,4	15,7	25,3
K	15,4	5,7	3,5	3,8	14,8	5,8	11,0	17,7

Table 34. Frequency distributions of all animals aged by the molar wear method in 1970 and 1971. Animals aged three years and less are omitted because most were aged by tooth replacement.

Age	1970		1971	
	Frequency	%	Frequency	%
3 - 4	71	27,2	47	26,7
4 - 5	57	21,8	39	22,2
5 - 6	40	15,3	28	15,9
6 - 7	33	12,6	20	11,4
7 - 8	24	9,2	18	10,2
8 - 9	19	7,3	11	6,3
9 - 10	8	3,1	6	3,4
10 - 11	6	2,3	4	2,3
11 - 12	2	0,8	2	1,1
12 +	1	0,4	1	0,6
Total	261	100,0	176	100,1

of a higher value greater than 0.9 in all cases.

8.3.6. Eye lens mass.

The eye lens mass is considered by Morris (1972) to be one of the more accurate age determination methods, because it is continually added to throughout life, and its situation is such that there is little if any attrition of material. Thus the mass should be proportional to age.

In so far as African mammals are concerned, comparatively little work on eye lens mass has been carried out. Laws (1967) found a high degree of correlation between age and eye lens mass in elephant, and concluded that the mass increase is rectilinear with respect to age. He also suggests that the technique may be a very useful supplement to ageing based on other criteria.

Fairall (1969) derived a curve for eye lens mass against age for a sample of 889 pairs of lenses of impala from Kruger National Park, amongst which were 12 known age animals. The relationship is distinctly convex, with the period of most rapid growth taking place up to the age of about 4,5 years.

No difference was detectable between the sexes in any one wear class, although Longhurst (1964) found significant differences in deer. For this reason all eye lens masses were pooled for the purpose of drawing up Table 35.

Comparison of the masses of paired lenses from a sample of 60 pairs revealed no significant differences between the individuals of a pair. The greatest difference was 4,3% of the

Table 35. The mean paired eye lens mass for each wear class of Mkuzi impala for the whole year, with standard errors of the means, standard deviations, and coefficients of variation (C.V.) of the samples.

Class	No. in sample	Mean ± S.E.	Standard deviation	C.V.
Yearling	116	1,0968 ± 0,005	0,050	4,6
Two-year	57	1,1911 ± 0.005	0,035	2,9
Nil	102	1,2582 ± 0,004	0,038	3,0
Light	149	1,3368 ± 0,002	0,024	1,8
Light/Moderate	191	1,3565 ± 0,003	0,044	3,2
Moderate	39	1,4479 ± 0,010	0,062	4,3
Moderate/Heavy	24	1,4478 ± 0,029	0,142	9,8
Heavy	36	1,4619 ± 0,011	0,068	4,7
Very heavy	7	1,5076 ± 0,022	0,059	3,9
Extra heavy	22	1,5181 ± 0,011	0,051	3,4
Extra heavy +	24	1,5356 ± 0,011	0,052	3,4

smaller mass. In 17 cases where only one lens was available therefore, the mass was doubled to obtain the "paired" value. A change in mass of 2 - 3% was found to take place over a period of about 15 minutes when the lenses were removed from the desiccator after cooling, due to the hygroscopic nature of the lens. Lenses were therefore removed from the desiccator immediately prior to weighing, and the inevitable error was limited still further by the speed with which it was possible to carry out the weighing procedure with the electrically operated balance.

The mean paired eye lens mass for each of the molar wear classes of 767 impala in Mkuzi is shown in Table 35. There is a definite increase in mass correlated with progressive wear, but actual ages cannot be derived from the data.

8.3.7. Horn growth checks and horn development.

An ageing technique that has not received a great deal of attention is the use of horn growth rings or "checks". This technique is based on the fact that the horns of antelope grow continuously from the base, and that there is a slowdown in this process at one or another time of the year, resulting in the formation of a ridge around the horn. Naturally, with age and the decreased rate of growth, these checks or ridges appear closer together, and may actually become indistinguishable as separate and identifiable entities. The growth checks must not be confused with the ridges that are characteristic of the horns of many species, and which usually develop in the first or second year of growth.

Authors who have used this technique for ageing, with varying degrees of success, are Brandborg (1955, quoted in Simpson 1971), Geist (1966), Caughley (1965), and Simpson (1971). Caughley (1965) described the method, and later used it (Caughley 1966) to derive mortality rates for Himalayan tahr in New Zealand. Simpson (1971) provided fairly conclusive evidence on the validity of this technique in ageing African ungulates. Examination of his photographs however, shows some of the difficulties in trying to separate the rings from one another.

Insufficient material from the present study was gathered to obtain conclusive evidence on this subject, and of the mere 43 pairs of horns collected, only 17 could be related to the mandibles. Eleven of these 17, for which horn rings could be clearly distinguished, showed 82% (9/11) correlation between the estimated age from the horn ring counts and age from the height of M_1. The two that did not "match" both had one more apparent ring than was expected from the age determined by the height of M_1. This error could have been due to the inadequacies of either of the methods, although the degree of correlation indicates that there may be some promise in the use of horn growth checks.

The conclusion that can be drawn in this regard is that the growth checks do provide a useful method of ageing, at least up to about five or six years of age, after which time it becomes difficult to distinguish individual checks. However, more data are necessary before doubt as to the validity of the technique can be dispelled.

No mention is made in the literature of the stage or time of year that the check in horn growth takes place. Simpson (1971) in supporting Geist (1966), stated that it is a seasonal phenomenon, without saying any more. Observations in this study, however, indicate that the check may occur early in the winter period. A very obvious ring, or fringe of frayed horn material, could be seen on the horns of juvenile males of six to eight months old. It became apparent in about July or August, when the horns had reached a length of about 12 cm. Its position, about 2 cm from the base and 8 - 10 cm from the tip of the horn, indicated that it must have been formed about a month or so earlier, coinciding with the peak of the rut and also with the time that most of the juveniles were being forcibly weaned during the disturbances associated with rutting behaviour. This then, is the first evidence for the timing of the check in horn growth, and a possible yardstick for future studies.

The form that the check takes in the first year is shown in sketch form in Figure 31.

Child (1964) and Spinage (1971) both illustrate the development of horns in impala, by which means it is possible to age the males quite reliably up to the age of two years. With the knowledge gained from a population with a restricted season of births and the consequent ability to age animals accurately, it is possible to say that the animals illustrated by Spinage (1971) as being approximately 18 months and two years old respectively, are in fact each about three months younger, provided of course that development in the two populations is similar.

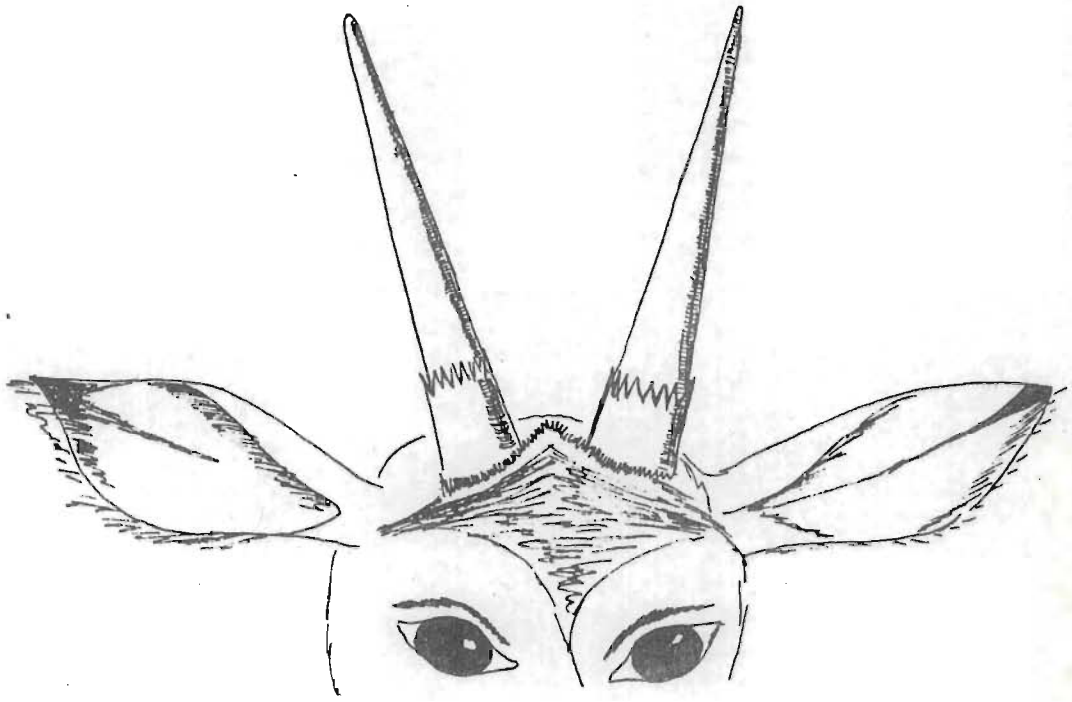

Figure 31. Sketch of the top of the head of a male impala approximately six months old, showing the form of the first growth check. Later wear renders the frill smooth and indistinguishable in older animals.

There is a great deal of variation in horn shape and size among adult males, and the size and conformation after two years of age cannot be used as a means of ageing at all.

8.3.8. Body mass.

The overall body mass of an animal is one of the commonest parameters that has been recorded by workers, first because of the comparative ease with which it may be measured, and secondly because it has been used in calculations of biomass in various parts of a species' range.

In a recent paper, Hanks et al (1976) compute a theoretical von Bertalanffy curve which indicates that male impala reach their asymptotic mass of 59,6 kg at the age of about five years. The formula used for plotting the curve is $w_t = W_\infty(1 - e^{-K(t - t_0)})3$

w_t = mass at age t.

W_∞ = asymptotic mass = 59,58 kg.

K = coefficient of catabolism = 0,95.

t = age of animal.

t_o = theorectical age at which the animal would have zero mass with the same growth pattern as that observed in later life = -0,83 years.

Up to the age of about three years the curve rises steeply.

Howells and Hanks (1975), in another study, find that males reach their asymptotic mass of 56,6 kg at about 4,5 years, and females reach theirs of 43,2 kg at about three years. The present study indicates that females reach

their maximum mass somewhat earlier: two to three year old animals have a mean mass of 41,1 kg, and the mean for all older females is 42,4 kg. In the case of males the mean mass of three to four year old animals is 52,6 kg against the mean for older animals of 55,2 kg, and it is concluded that they reach maximum mass after four years.

As a means of ageing, body mass is completely unreliable. In a sample of yearling males from September 1971 for instance, mass varied from 34 kg to 53 kg.

8.4. Discussion.

Having established what would seem to be a valid ageing technique, it is possible to relate the data obtained by other means to the ages deduced from molar height. The other methods may therefore be evaluated.

8.4.1. Molar wear.

Table 36 illustrates the relationship between age and molar wear. As can be seen, the range of ages in each wear class is considerable, although the median age of each class does show a trend. Nevertheless, the unreliability of the molar wear ageing method is amply demonstrated, and bears out what has been shown for deer in America (Robinette et al 1957, Erickson et al 1970). The ageing of impala on the basis of tooth wear, as carried out by Roettcher and Hofmann (1970), Spinage (1971), and Cowley (1975), is largely invalidated as a result of this finding, not so much in that the results are

Table 36. Distribution of wear classes of impala in Mkuzi in relation to age determined by molar height. (The median age in each wear class is designated by *).

Age (years)	Wear class								
	Nil	L	L/M	M	M/H	H	VH	EH	EH+
2-3	56*	56	10						
3-4	23	153*	20	1					
4-5		67*	56	3					
5-6		5	57*	6	4	1	1	1	1
6-7		1	26	13*	9		2		
7-8			25	6	8*	10	1	4	
8-9			6	7	3	4*		3	
9-10			2		4	3	1	2	8
10-11						4	2		7*
11-12								1	4
12+									2
Total	79	282	202	36	28	22	7	11	22

inaccurate, but that the range of ages over which the various degrees of wear occur is too great for the allocation of ages to be meaningful.

Generally speaking, the technique of molar surface wear tends to overestimate the age. For example, it is assumed by Roettcher et al (1970) and by Cowley (1975) that animals with all surfaces worn smooth are 12 years old or older, whereas Table 36 shows that this may occur in animals as young as 9 - 10 years old.

Figure 32 illustrates the rate at which the height of the first lower molar decreases, i.e. the rate of wear on the tooth. From the curve, values for which are calculated by the formula

$$R_x = \frac{h_{x-1} - h_x}{h_{x-1}}$$

where R_x is the rate at age x and h_x is the height at age x, it can be seen that the rate of wear is very rapid up to the age of three years, after which it slows down to a minimum at age six years. After that it increases again exponentially. This is in accordance with the conclusion reached earlier (Chapter 8.3.5.) that wear is initially high, but decreases as M_2 and M_3 enter the arc of attrition. It suggests that M_2 and M_3 become fully operational after the age of three years. The period of lowest rate of wear is between 4,5 and 7,5 years and it is probably true to say that this is the "physiologically prime" age.

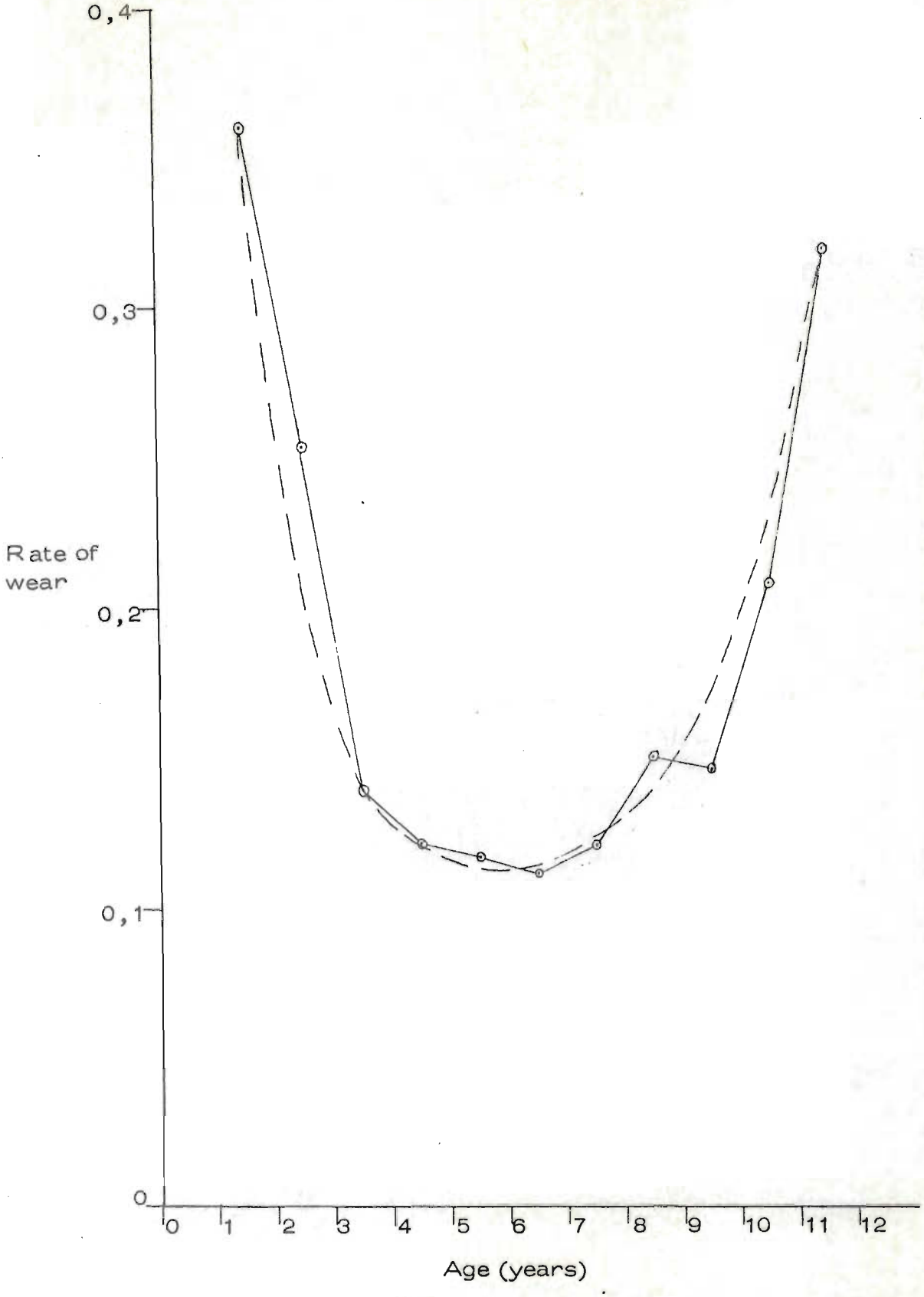

Figure 32. Rate of wear of the first lower molar of Mkuzi impala related to age in years. The dotted line has been fitted by eye. For calculation see the text.

8.4.2. Incisor index.

When the incisor index as analysed in Table 29 is plotted against the age classes derived by means of molar height, the two samples show a close correlation with each other. However, the distribution of the classes in relation to age derived from molar height shows even greater variation than does that of molar wear classes. However, there is fairly close correlation up to the age of about six years, after which the index becomes very unreliable.

8.4.3. Eye lens mass.

The regression of eye lens mass on age is shown graphically in Figure 33. There is considerable overlap between age classes in standard deviations, but the trend is obvious, with a continuous increase right through life - initially rapid, but slowing down after the age of three years.

The only other known studies on the eye lens mass of impala are those of Fairall (1969) and Howells and Hanks (1975). They give very few details of the actual values obtained, but it is possible to deduce from Fairall's results that the heaviest lens, that from an assumed 12-year-old animal, weighs about 0,8 g. Although not actually stated, it is presumed that this is the mass of only one lens, so that the paired mass would be about 1,6 g which is comparable with the heaviest pair of lenses obtained in Mkuzi of 1,6520 g in a 10-year-old animal. The mass of the 3,5 year old, known age animal is about 0,65 g (paired 1,30 g) and that of a 4,5 year old about 0,73 g (paired 1,46 g). The first of these

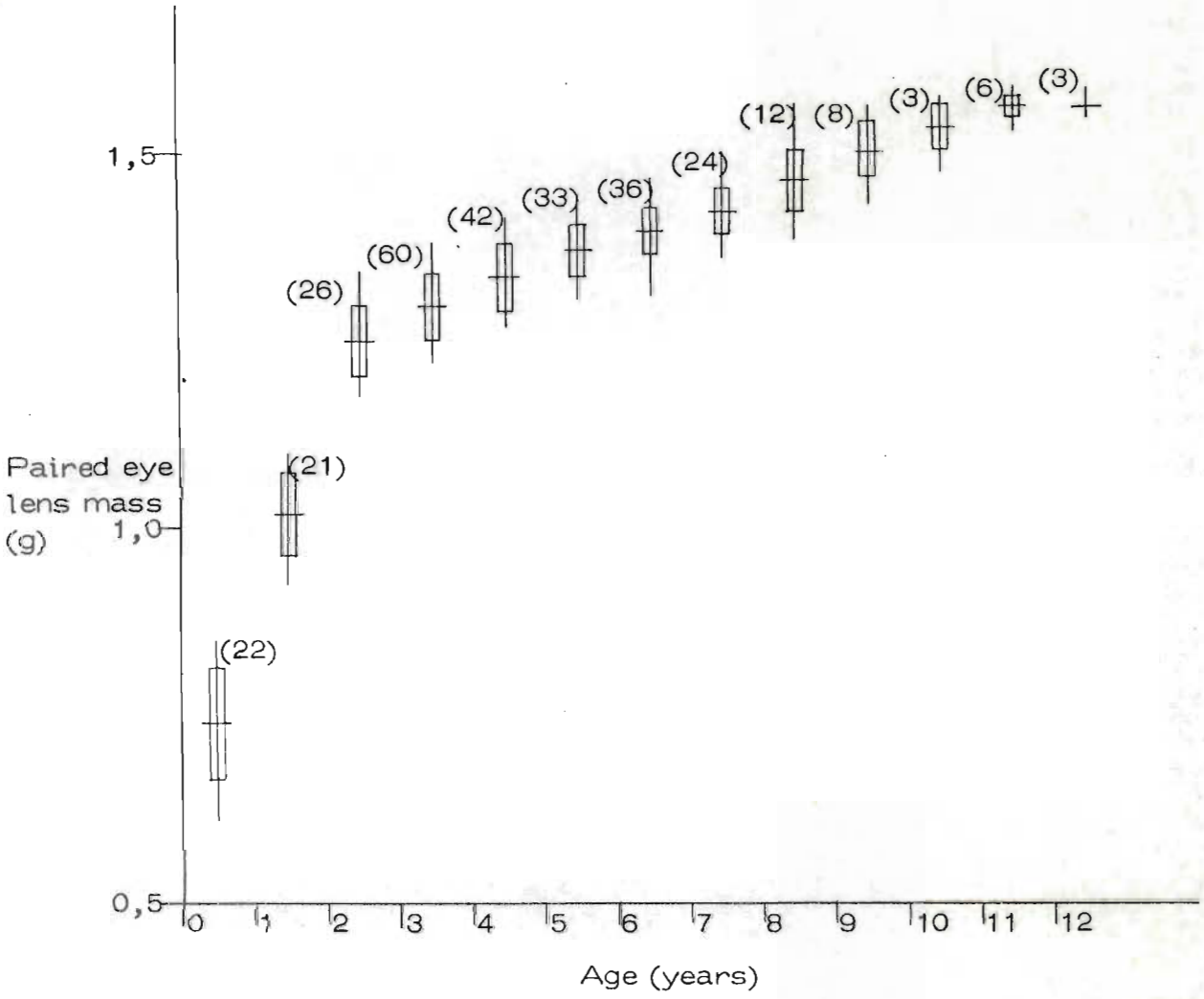

Figure 33. Paired eye lens mass in grams plotted against the age derived from the molar height of the August/September sample of Mkuzi impala. The mean value at each age is shown as a horizontal line, the standard deviations by a rectangular box, the range by a vertical line, and the number in the sample is shown in parentheses.

is well within the limits of animals of the same age in Mkuzi, but the latter is more akin to an eight year old. Up to two years of age, Fairall's (1969) curve closely resembles that shown here; after that age his curve is simply extrapolated.

The results of Howells and Hanks (1975) indicate only that there is considerable overlap between the sexes (if indeed any difference exists at all) and that there is considerable overlap between most of the age classes above three years. They conclude that lens mass alone is only of limited value in estimating age of individuals, but that it does support the validity of chronological ages derived by the technique of Jarman (1973, unpublished).

CHAPTER 9

REPRODUCTION

9.1. Introduction.

Various aspects of the reproductive biology of impala have been reported on by workers in all parts of the species range, from which a comprehensive picture of the subject has emerged. Much of this work was synthesised by Vincent (1972), in reporting on a one-year study of the Mkuzi population. The results reported here are a more comprehensive continuation of that study.

9.2. Method.

9.2.1. Males.

The testes of all cropped males were removed as soon as possible after death and the mass of each pair, complete with epididymides, weighed to the nearest 0,1 g, on a triple beam balance. The tunica vaginalis was removed and the spermatic cord severed close to the head of the epididymis before measuring.

The age at which the asymptotic mass was reached was determined on the basis of molar wear.

9.2.2. Females.

The ovaries and uterus were removed from each female as soon as possible after death and preserved in 10% formalin for later examination. Where possible any foetus was retained, but when it reached such a size as to be impractical to preserve it was removed from the uterus, sexed and the mass and dimensions were measured.

In later examination, the site of implantation was recorded, and each ovary was removed in turn and weighed. It was then sectioned by hand at intervals of between 0,5 and 1,0 mm and the number of follicles and corpora albicantia were counted. The diameter of the largest follicle and that of any corpus luteum was measured to the nearest 0,01 mm, with a vernier caliper, and the location of each was recorded, i.e. in the left or right ovary.

9.2.3. Sex ratio.

The sex of the foetus was recorded wherever possible from about the second month of pregnancy onwards.

The sex and age of all individuals seen in the field during the course of the road strip censussing was recorded whenever possible, and these data were used in the determination of sex ratios.

9.3. Results : males.

9.3.1. Age at maturity.

Kerr (1965) provides evidence that yearling ("immature") males breed successfully at between 17 and 18 months of age in a seasonally breeding population. A number of impala, translocated to an inpopulated area, produced young which could only have been sired by the immature males in the group; no adults were present. However Kerr (1965) concludes that males may become physiologically capable of fertilising a female at about 13 months of age.

Hanks et al (1976), on the other hand, report that full spermatogenic activity in impala from western Rhodesia, where breeding is also seasonal, occurs from about 15 months of age. They find no decline in physiological sexual activity with age.

No histological or physiological work was carried out on the Mkuzi population, so that there is no direct evidence to confirm the findings of other workers. However, despite the early stage at which impala are capable of fertilisation it is unlikely than more than a few, if any, actually achieve successful mating before three or four years of age, at least.

It was stated in Chapter 6.3.1. that of 14 territorial males examined one was 3,5 years old, and two were over seven years. It is probable that only territorial males succeed in mating, so that most breed at between 4,5 and 6,5 years of age.

The mean paired testes mass of animals in different year classes was determined from samples collected throughout the year. Up to three years of age, significant changes were apparent between year classes in most months, but above that the differences are not significant. The age at which asymptotic mass is reached is therefore between three and four years, which agrees closely with the findings of Hanks et al (1976) that testis growth continues until about four years of age, particularly if it is assumed that their ageing method tends to overestimate age as discussed in Chapter 8.3.2. The mean monthly testis mass of impala of various ages is illustrated in Figure 34.

9.3.2. Seasonal changes.

a) Testis mass

Bramley and Neaves (1972) studied a population of impala in East Africa, where breeding is not seasonal, and apparently did not test for seasonal changes in testis mass. It is therefore not known whether any such changes do occur there, but it is unlikely in view of the year-round breeding activity.

Several studies have been undertaken on the seasonally breeding southern populations, all of which show seasonal changes in testis mass. Anderson (1965) reports that the mean paired mass of mature animals in Hluhluwe Game Reserve varied between a high of 133 g in March and 66 g in July, while the maximum was 172 g (February) and the minimum 49 g (June).

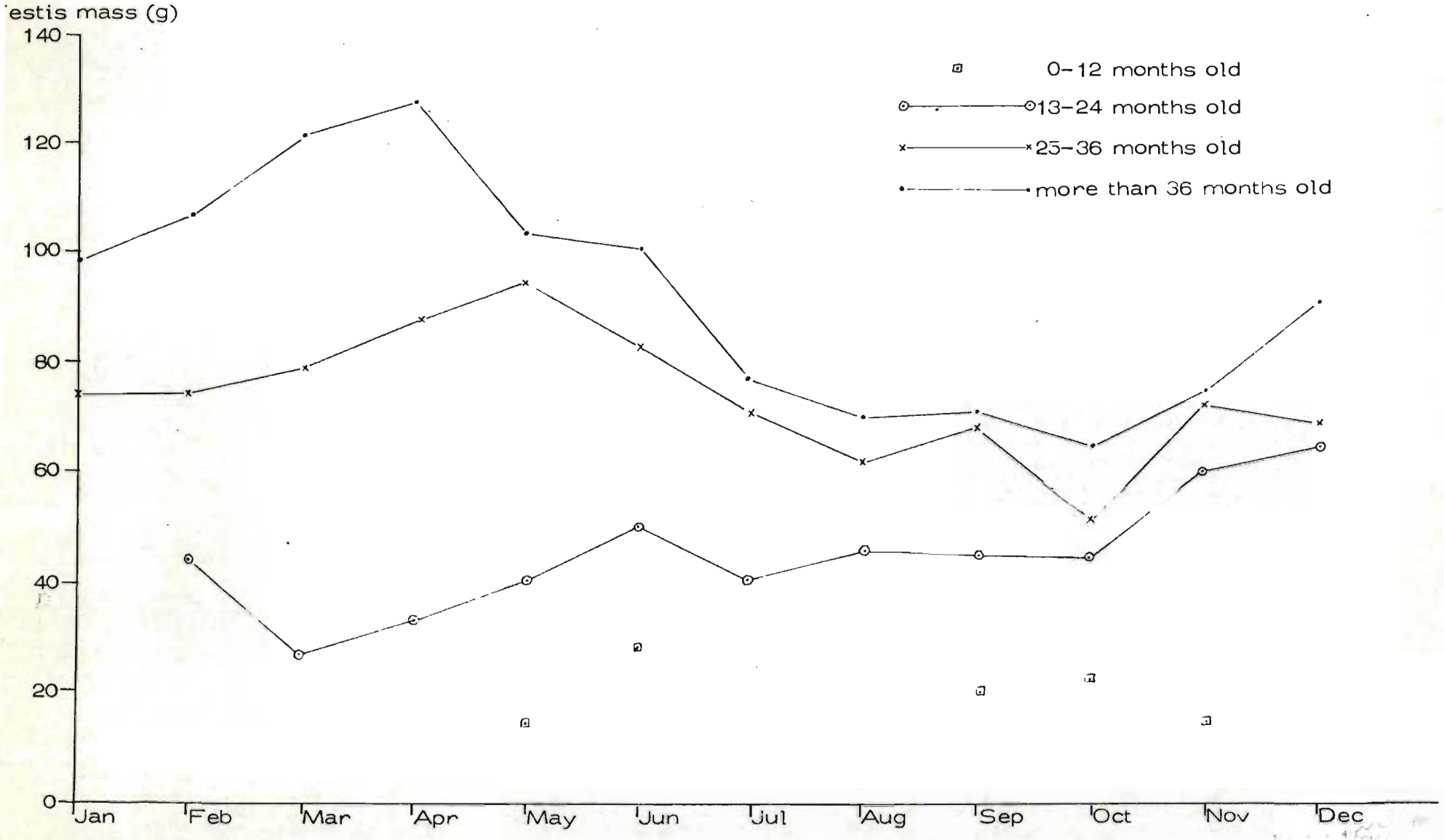

Figure 34. Seasonal changes in mean paired testis mass of Mkuzi impala of different ages.

Hanks et al (1976) find an even greater difference, the mean mass varying from about 97 g in February to about 32 g in September (the much lower means are probably because younger animals are included). The apparent inclusion of younger animals also resulted in more fluctuations between February and June than are recorded elsewhere.

Skinner (1971 a, b) records similar changes, with a maximum of about 122 g in February and a minimum of about 60 g in September. These values compare closely with the results of Anderson (1965).

Vincent (1972) reports a mean maximum paired testis mass in animals over 30 months old of 118,3 g in April and a mean minimum of 59,6 g in October in a sample of 163 animals collected in 1970.

The results of the present, more complete, study, with a sample of 401 males over three years old, confirm the earlier findings, with a mean mass of 127,5 g in April and 64,8 in October, as seen in Figure 34.

A common feature of all these studies is the fact that the mean maximum mass is consistently about twice the mean minimum. Another feature is that the maximum is reached before the peak of the rut. This is pointed out by Skinner (1971 a, b), who also found that the peak incidence of sperm reserves coincided with the rut. This suggests that there is a correlation and that the testis mass is associated with sperm production. Why it is that the peak of testis mass should be

reached later in Mkuzi than has been reported elsewhere, is not known.

The peak in testis mass in animals less than three years old occurs later than it does in older animals, as can be seen in Figure 34. A possible explanation for this is that the behaviour of fully mature animals associated with the rut produces a hormonal reaction in the younger animals, which has the effect of increasing their testicular activity. The functional mechanism of this feature is not clear.

b) Other parameters.

Skinner (1971b) carried out histological and histochemical examination of the testes and accessory sex organs of impala, while Hanks et al (1976) examined the growth and development of these reproductive organs. The latter report that, although the mass of the epididymides and seminal vesicles and the diameter of the seminiferous tubules reach their asymptotic peak during the fourth year, coinciding with asymptotic testis mass, the bulbo-urethral (Cowper's) glands remain small until slightly later. Their most important conclusions are that the accessory sex organs show "no evidence of a peak of activity in any one age group, and no indication of a significant decline in reproductive activity in old age". The diameter of the seminiferous tubules decreases slightly in September/October, coinciding with the mean minimum testis mass.

Skinner (1971b), on the other hand, concludes that the production of androgens declines rapidly after the rut, because

there was a marked decrease in the presence of fructose and citric acid found in the accessory glands and a correlation between these parameters in many other ruminants. This is apparently a function of the lowering of nutritional levels.

Spermatogenesis does not cease altogether at any time, so that in this sense the impala male is capable of fertilisation throughout the year, even in the seasonally breeding populations. No reference to physiological changes occurring in non-seasonally breeding ungulates has been found.

9.3.3. Individual differences.

The difference in mean testis mass between a sample of 13 animals which were almost certainly territorial and 57 others which were in bachelor herds, all collected in May, was very small, and it is concluded that the possession of a territory is certainly unrelated to testis mass, and probably also to the activity of other sex organs. The actual mean paired testis mass in the two groups was 104,2 g for territorial males and 103,1 g for bachelor males, $t = 1,15$, d.f. $= 68$, $P > 0,3$.

This finding agrees with that of Bramley and Neaves (1972), who show that there is no significant difference in the testis mass of territorial and bachelor males in an East African population which breeds throughout the year. They do, however, find a significant difference in testosterone levels between the two groups, and conclude that this is a result of the higher level of overt sexual activity in territorial males, rather than the cause.

9.4. Results : females.

9.4.1. Age at maturity.

Vincent (1972) discusses at some length the age at which female impala breed for the first time. The majority of authors have not reported conception in juveniles (Kerr 1965, Dasmann and Mossman 1962b, Child 1968), but a small proportion of juveniles in Mkuzi (I.B. Stewart, unpublished data, Natal Parks Board files) are presumed to have been pregnant. One of 27 was in fact found to be pregnant, and a further 10 out of 32 yearlings were lactating.

No further evidence has emerged from the literature, although Vincent (1972) reports that in the 1970 sample of Mkuzi impala one out of seven (14,3%) juveniles (less than one year old) was pregnant and in addition six out of 20 (30%) yearlings (12 - 24 months) had corpora albicantia, suggesting that they had borne young as juveniles.

Jarman (in litt.) states that a small percentage of yearling impala in the Zambezi valley was recorded as lactating, providing further evidence of sexual maturity during the first year of life.

In the 12 - 24 month age group (yearlings), I.B. Stewart (op. cit.) reports that 10 out of 32 (31,3%) were pregnant, and Vincent (1972) records seven out of seven (100%) to be pregnant. Of these latter, one foetus was being resorbed, reducing the pregnancy rate to 85,7%. Similar figures for yearlings are recorded elsewhere : Dasmann & Mossman

(1962b) 11 out of 13 (84,6%); Child (1968) seven out of eight (87,5%). Mentis (1972) reports that between 30% and 87% of females in the Kruger National Park calve for the first time at two years of age, while Joubert (1971) on the other hand suggests that none of ten yearling South West African black-faced impala translocated was pregnant.

In East Africa, Kayanja (1969) observed that females conceive for the first time at about 12 months of age.

In the present study, 258 female impala were examined in a period of three years, 1970 - 1972. Of these, 22 were juveniles, 43 were yearlings, and 193 were adults. It was possible to use only 115 of these for pregnancy determinations, as they were collected between June and November. Results are as follows:

Juveniles	1/9	pregnant	11,1%
Yearlings	13/15	"	86,7%
Adults	87/91	"	95,6%

In addition to those recorded directly as being pregnant, two of the 24 yearlings in this sample (8,3%) and 37 out of 43 (86,0%) animals aged between two and three years, had corpora albicantia which suggested that they had been pregnant in the previous year.

Thus it is concluded that an average of 9,1% of juveniles, 86,2% of yearlings, and 95,6% of adults made up the active female breeding segment of the population during the study period.

9.4.2. Seasonal changes in the ovary.

Kayanja (1969) has reported on ovarian changes in East African impala, which have no strict breeding season, although two main breeding peaks are evident during the year. The basic histological changes he describes can safely be assumed to apply to the species generally.

Vincent (1972) describes the gross characteristics of the impala ovary for the Mkuzi population, and further examination of a larger sample confirms his earlier findings. There is an initially large increase in the number of large (> 2 mm) follicles between December and April, and a sharp decline from June to October. This is a similar pattern to that found by Fairall (1972). The mean diameter of these follicles also increases up to April, with a second "peak" in September.

The increase in number of follicles coincides with the peak of the rutting season, whilst the periods in which the follicles are largest coincide with the main rutting season and with the period in which there is a secondary peak in the incidence of territorial males, as described in Chapter 6.2.2. The reasons for and significance of this coincidence are not known.

Whereas from Kayanja's (1969) text figure 1 it is apparent that the largest follicles are about 7,0 mm in diameter, the largest follicle recorded in Mkuzi had a diameter of only 6,3 mm. The largest mean follicle size recorded by Fairall (1972) is 4,8 mm - collected in March, although he adds that follicles larger than 5 mm in diameter are only found in April and May.

The follicular atresia dscribed by Kayanja, in which cells are sloughed off into the atrium of the follicle, is most marked in specimens collected between 14 and 27 May in all three years, with a few showing this condition in an advanced form in early June. In some of these latter cases it is clear that formation of corpora lutea is taking place.

The presence of a corpus luteum is associated with pregnancy, and in the early stages, when embryos were not clear from gross examination of the uterus, it was taken as a sign of pregnancy. Only animals collected from June onwards were examined to establish whether they were pregnant or not.

In the earlier study the mean diameter of corpora lutea was shown to increase from 5,88 mm in May to 7,52 mm in August. With samples available in September, October and November in this study, the mean diameter is shown to reach a maximum of 8,1 mm in October (n = 3), and to remain unchanged at 8,0 mm (n = 2) through November. After parturition, a single specimen collected in December shows a rapid shrinking of luteinised material (corpus luteum) to an irregular shape.

Vincent (1972) showed that corpora albicantia, although present in nearly all animals over three years of age, are not necessarily a reliable indicator of the number of previous pregnancies that have taken place. Using the gross method of examination this conclusion is confirmed by the present sample, in which the number of corpora albicantia recorded is in no way

correlated with estimated age. It is possible that a more thorough histological investigation would produce more reliable results, as were obtained by Watson (1969) in wildebeest.

9.4.3. Gestation period.

The gestation period of impala has been well determined, and the evidence from various sources is collated by Mentis (1972). The most reliable evidence, from direct observation, points to a gestation period which varies between 194 and 204 days. The figure of 204 days, quoted by Basch (1964), is for two "young" females, and the question immediately arises whether age of the female has any influence on the gestation period.

On the evidence provided by Mentis (1972) based on six direct observations, the mean gestation period is 199 days. Based on evidence from ovarian analysis in the Mkuzi study, the median date of conception is 21 May, giving the median date of parturition as 6 December.

9.4.4. Foetal implantation.

Mossman and Mossman (1962) recorded implantation only in the right uterine horn in impala, despite almost equal ovulation from the left and right ovaries. In a smaller sample the same situation is found by Hofmeyr and Skinner (1969) in impala from the same locality, namely Rhodesia.

In 101 pregnant uteri from Mkuzi examined over a three

year period there is no record of implantation in the left horn. Furthermore, all non-pregnant uteri examined in which a difference could be detected had the right horn more swollen than the left, with the single exception described by Vincent (1972).

Of the 97 corpora lutea of pregnancy that were found, 51 were in the left ovary and 46 in the right. This difference is not significant (chi squared = 0,26, d.f. = 1, $P > 0,5$). Thus ovulation takes place with equal frequency from left and right ovaries.

One case of foetal resorption was recorded as described in Chapter 9.4.1.

9.4.5. Foetal development.

The growth of the impala foetus is illustrated by Vincent (1972) for a sample of 32 specimens collected in 1970. With the addition of 67 specimens from the 1971 and 1972 samples, the regression coefficient of the cube root of foetal mass on foetal age becomes $Y = -3,35 + 0,101x$ and the general equation of Huggett and Widdas (1952) for foetal growth becomes $W^{1/3} = 0,101(t - 32,5)$, where $W^{1/3}$ is the cube root of foetal mass, and t is the foetal age in days. The coefficient a (0,101) is the point at which the projected regression line intercepts the abscissa.

The regression is shown in Figure 35. From it the foetal mass at parturition is estimated as 4,74 kg ($W^{1/3} = 1,68$).

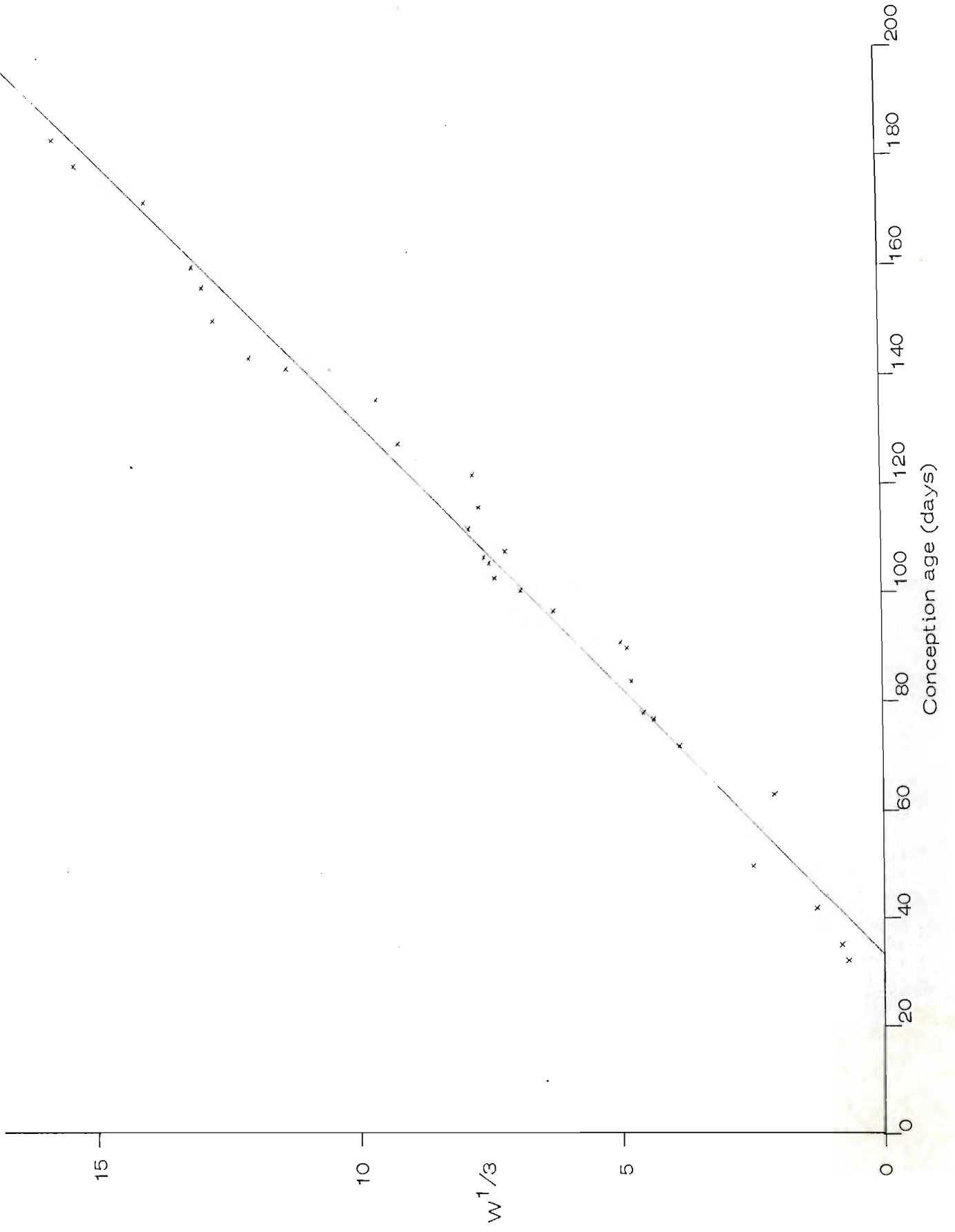

Figure 35. Regression of cube root of foetal mass ($W^{1/3}$) on foetal age in days since conception for a sample of Mkuzi impala obtained in 1969, 1970 and 1971. The regression equation is $Y = -3,35 + 0,101X$.

9.5. Sex ratio.

The sex ratio of impala in various populations is summarised by Vincent (1972), from evidence gleaned from the literature. Most populations have a sex ratio in the region of one male to two females, with some regional variation. However, variations at any one locality are apparently sometimes confused by seasonal changes due to one or another factor.

9.5.1. Seasonal changes.

Hirst (1969b) provides data on the sex ratio of impala in Timbavati, adjacent to the Kruger National Park, during two periods of the year over a number of years. The mean sex ratio of all animals of one year and older is 1 male : 2,77 females in April/May and 1 : 1,90 in November/December.

Jarman (1972) gives ratios for three periods of the year in the Zambesi flood plain. For animals over one year of age these are:

April	1 : 1,55
August	1 : 1,14
October	1 : 1,33

The differences between these samples are explained by differential movement of the sexes out of the study area during the dry period. More females moved away, accounting for the lower proportions recorded in August and October.

In Mkuzi, the sex ratios of impala over one year of age sampled in each month of the sampling period are shown in Figure 36. Also shown is the mean sex ratio for each of the

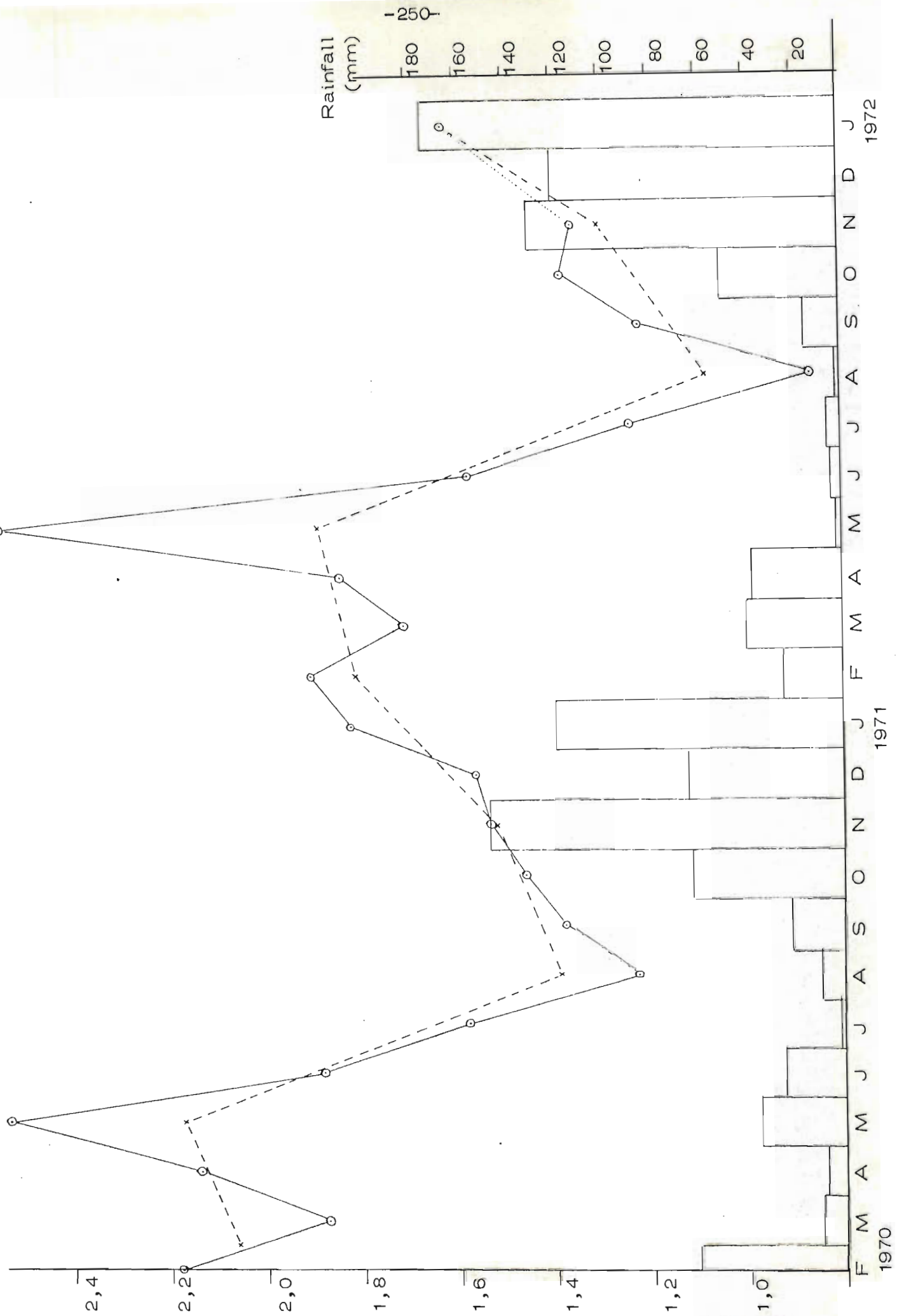

Figure 36. Monthly sex ratios of impala sampled in Mkuzi in 1970 and 1971 (⊙——⊙) and the three-monthly mean sex ratios over this period (×--------×). The sex ratio is expressed as females/male. The monthly rainfall figures are shown as a histogram aver-

three month periods representing the "seasons" in Mkuzi - late summer (January - March), early winter (April - June), late winter (July to September), and early summer (October - December). The sex ratios are expressed as females/male, and the monthly rainfall is included to show the dry periods.

There is a distinct correlation between rainfall and sex ratio. The preponderance of males in the dry months suggests that there is an exodus of females from the study area. This was discussed in Chapter 7.2.5, but no clear pattern emerged at that stage.

The pattern of change in the sex ratio shows a steady increase in the proportion of females from September, reaching its peak at the time of the rut in May. This is followed by a sharp drop over the next three months. The trend is similar in each of the two years of sampling, which reinforces the possibility that changes in sex ratio are due to some inherent factor, rather than to sampling error or environmental factors.

9.5.2. Changes with age.

a) At birth.

The sex ratio of any animal at birth is not an easy parameter to determine. In the literature there are two records for impala: Brand (1963) noted that, of a total of 120 impala born in a zoo, 50 were males and 70 were females, i.e. a sex ratio of 1 : 1,40. Mossman and Mossman (1962) recorded 25 males and 34 females (1 : 1,36) in a sample of foetuses old enough to be sexed in a population from Rhodesia. In the

present study, 50 foetuses were sexed, of which 21 were males and 29 females, giving a ratio of 1 : 1,38. The combined figures from all these samples give a ratio of 1 : 1,39. It is therefore concluded that the foetal sex ratio of impala is 1 : 1,4, and assumed that the ratio at birth is the same.

The sex ratio of each one of these samples is not significantly different from parity, but if all the samples are combined to give 96 males and 133 females, the ratio does deviate significantly (chi squared = 5,98, d.f. = 1, $P < 0,025$). Although such a procedure is not strictly permissible, the consistency of the ratio in the three different samples strongly suggests that it is real.

On the other hand Smith (1975) recorded a foetal sex ratio of 1 : 0,66 in a sample of 149 from the Zambezi valley in Rhodesia. This is significantly different from parity (chi square = 6,4), but obviously in favour of males.

b) Juveniles.

The sexing of juvenile impala is not possible in the field until the age of about four months, when the horns become apparent. In the count held in the first week of April 1971, 82% of the juveniles were sexed. In the count held in the third week of April 1970, it was possible to sex all juveniles. On the other hand, after September it was not possible reliably to separate juvenile females from older animals.

The results for the period from April to September are shown in Table 37, from which it is clear that there is an

Table 37. Juvenile sex ratio of impala in Mkuzi between April and September for the two years 1970 and 1971. Samples from road strip counts, augmented by counts at water-holes. Ratio expressed as male:female.

Month	1970			1971			Both years		
	M	F	Ratio	M	F	Ratio	M	F	Ratio
April	218	320	1:1,47	247	342	1:1,38	465	662	1:1,42
May	212	316	1:1,49	165	206	1:1,25	377	522	1:1,38
June	354	556	1:1,57	264	404	1:1,53	618	960	1:1,55
July	227	330	1:1,45	247	409	1:1,66	474	739	1:1,56
August	182	291	1:1,60	200	355	1:1,78	382	646	1:1,69
September	218	386	1:1,77	238	438	1:1,84	456	824	1:1,81

increase in the proportion of females with age. This suggests that there is a higher mortality of males during this period, in the approximate proportion of four males to three females.

In July 1968 the sex ratio of juveniles was 1 : 0,78 (University of Natal Wildlife Society 1968).

The sex ratio of juveniles recorded by Smith (1975) in a culling operation is the Zambezi valley in July over two successive years consistently favoured males (1 : 0,84 in 1969 and 1 : 0,82 in 1970). When compared with the foetal sex ratio of 1 : 0,66, this too suggests a higher mortality of males in the first seven months of life, also in the approximate proportions of four males to three females.

c) Adults and yearlings.

The sex ratios of impala over ten months of age are shown in Figure 36, and are discussed in Chapter 9.5.1. The sex ratios of individual age classes are not really a meaningful parameter, as long as the overall ratio in the breeding population is obtainable. This will become evident in the treatment of life tables in Chapter 12.

In a survey carried out during the first five days of July 1968 (University of Natal Wildlife Society 1968), the sex ratio of adults and immatures was found to be 1 : 1,9, which resembles quite closely the results for June in this study.

Smith (1975) recorded a sex ratio of parity in the Zambezi valley in July.

9.6. Discussion.

9.6.1. Age at maturity.

The age at which females first conceive is a critical factor in population dynamics, particularly in seasonally breeding populations, where early maturity may mean the difference of a whole year.

In a species such as impala, which normally bears its first young at two years of age, earlier maturation will result in first breeding at one year. The proportion of animals of this age is usually quite high under the same favourable conditions that lead to early maturity, so that there is a markedly higher proportion of young animals which results in a sharp rise in the rate of increase.

The conditions which lead to variations in the age at maturity are not clear. Child (1968) concluded from his observations that a temporary low plane of nutrition does not affect sexual maturity in females, although in the longer term it may retard physical growth and so delay maturity. He found that under conditions of some nutritional stress, seven out of nine (77,8%) yearling females conceived and would have given birth at two years of age. Dasmann and Mossman (1962b) recorded 11 out of 13 (84,6%) yearlings that were pregnant. These are small samples but the proportions are similar to the 86,2% recorded in Mkuzi.

The effect on population dynamics of any change in the age at maturity of males is not as great as it is in females.

9.6.2. Seasonal cycle.

Bramley and Neaves (1972) concluded that hormone levels in male impala are influenced by territorial behaviour and not vice versa. If this is the case then a possible reason for territorial behaviour is that it is an advanced form of psychological dominance brought on by some environmental factor such as day length or nutritional status (Skinner 1971a). This may account for the seasonal incidence of territoriality in populations at higher latitudes and the year-round territoriality in populations nearer the equator. However, not all seasonally breeding populations exhibit territoriality; Warren (1974) found, for instance, that it did not occur in his study area where impala density is low. Thus density may be a contributory factor to the incidence of territoriality, and this form of behaviour may simply be an adaptation to ensure optimum breeding success at high densities.

In female impala follicles of varying sizes are present in the ovary at all times of the year, yet these do not normally develop except during the rutting season. The cycle of testicular activity in males and the behaviour associated with it therefore possibly acts psychosomatically on the female, causing ovulation to take place at the time when territorial behaviour is at its peak. On the other hand, in East African impala ovulation takes place throughout the year (Kayanja 1969) as does male territorial behaviour.

The interaction of the various factors which influence seasonal breeding, including the possibility of some effect of the lunar cycle, to bring about synchronisation of the male

and female reproductive cycles, needs a lot more careful study. What is certain though is that the evolutionary significance and value of the pronounced seasonal breeding is that the young are born at a time when the habitat and environmental factors are the most favourable, ensuring the best possible survival rate.

9.6.3. Sex ratios.

The seasonally low incidence of females in the population coincides with the period at which the exodus of adult females inferred in Chapter 7.3.4. takes place. The change in sex ratio during the latter part of the dry season is therefore attributed to this movement. The reason for the exodus is probably that the animals go in search of more favourable habitat conditions along the food plain of the Msunduze river in the south of Nxwala State Land. This is comparable with the presence of a concentration of ungulates on the Zambezi flood plain which was reported by Jarman (1972).

Jarman (1970) noted that males tend to be more sedentary than females, and this is supported by the findings of this study in which it is predominantly females that emigrate. They do however, return to their home range in East Africa and it is assumed that they do in Mkuzi too.

The sex ratio of adult and immature animals was reported by Smith (1975) to be parity in a population in the Zambezi valley. However the samples were taken during the dry season when movement of females may have affected the structure. Furthermore the sample consisted of shot

animals and there may have been some bias by the hunters towards shooting males. He does not provide comparative figures for the sex ratio of the standing population.

Brooks (1975) has discussed the progressive change in sex ratio in Mkuzi impala between 1963 and 1973, and concluded that the sharp rise in the proportion of males in 1973 was attributable to the removal in game control programmes of a preponderance of females. Certainly in the preceding four years a total of 2 873 males and 6 936 females, a ratio of 1 : 2,4, was removed giving reason enough for this conclusion. However, in the sampling in 1970 and 1971, when a ratio of 1 : 2,2 was removed (1 312 males and 2 947 females), no significant trend in sex ratios was evident in the sample, other than that already alluded to. This change was not associated with the capture programme, for the ratio stabilised to its original level again in early summer.

The samples used by Brooks (1975) were taken in May and June 1973, following the capture, but also coinciding with the rut. However the sample in June 1971, in the present study, also followed large-scale capture of about 1 400 females and juveniles and 300 males, yet the sample sex ratio did not show a downward trend of females, nor did that in September 1970, after capture in that year. It is therefore concluded that capture does not have any significant effect on sex ratios, and the findings and conclusion of Brooks (1975) cannot be supported. Furthermore his sample of 1 574 animals is really inadequate to determine sex ratio with any degree of confidence.

9.6.4. Seasonal breeding.

Vincent (1972) discussed the breeding seasons of impala over most of the species' range in Africa, and concluded that there was an apparent gradient from north to south, with a tendency for the peak of parturition to be later and sharper in the most southern populations, with no strict season near or on the equator. There is even some difference between impala in the Kruger National Park, which lies between about 22°30' and 25°30' south latitude, and Mkuzi at about 27°30' S. In Kruger National Park, the season of births is from the beginning of November to the end of December (Fairall 1968) and in Mkuzi it is over about two to three weeks from late November to mid-December. The first recorded births in 1970 and 1971 were on 20 and 22 November respectively and the median date was estimated to have fallen within the first week of December.

Spinage (1973) discussed the influence of photoperiodism on conception in a number of African ungulates and concluded that impala have a short-day response, with most conceptions taking place as the length of daylight decreases. This is somewhat at odds with the discussion of Vincent (1972) as a result of which it might be expected that the southernmost populations would in fact have an earlier season than northern populations if the actual length of daylight is the critical factor.

The more concentrated breeding season of southern populations may also be looked at in the context of photoperiodism, for in the higher latitudes the length of daylight changes more rapidly than it does in the lower

latitudes. This suggests that changes in day length may be more important than actual day length in determining the duration of breeding seasons. However, more experimental evidence is needed to confirm this and to determine the factors influencing the timing of breeding.

CHAPTER 10

AGE STRUCTURE

10.1. Methods.

The categories of impala defined at the start of Chapter 4 were used in the field studies, both during the course of the road strip censussing and in observation at waterholes. More refined and comprehensive ageing was achieved in respect of material from dead animals by the methods described in Chapter 8, based on tooth eruption and wear.

It was not possible to distinguish juvenile males from females in the field for the first few months of life, and until the horns became visible at about three to four months of age. It was not easy under field conditions to distinguish juvenile females from the age of nine months from yearling and adult females, unless they happened to stand long enough alongside one another for comparison to be made; this did not often happen, and for this reason, after September no effort was made to distinguish juvenile females from others during the course of the censussing. The number of impala coming to the waterholes to drink after the onset of the first substantial rains in October precluded the use of waterhole counts as a means of obtaining samples from which to determine age ratios.

10.2. Results.

10.2.1. Road strip samples.

The numbers of each of the various age and sex classes that were distinguishable in the field are shown in Table 38 for each of the counts that were conducted throughout the two years of sampling. There is nothing particularly significant about these results, although a reduction in the numbers of juveniles seen would be expected if any mortality of, or predation on, that class took place in the first year, or even in the first few months of life. This was not the case, at least after January, and in fact, from that month onward there was no significant reduction in numbers of juveniles. During late winter, coinciding with the emigration of animals, there was actually a slight increase in the proportion of juveniles relative to the other age groups. This seems to indicate that the females that took part in the emigration were the non-breeding ones. Had it been the breeding females that moved out of the study area their young would have accompanied them, and the porportion of juveniles would not have shown the increase that was observed.

The difference in the proportions of the various age and sex classes between the two years was very small, as can be seen from Table 38. Furthermore, the same pattern is evident in both 1970 and 1971. For instance, there was a higher percentage of adult males in July and August of both years than at other times. More important, however, is the fact that the percentage of juveniles in the two samples was essentially the same - a feature which will be discussed

Table 38. Relative numbers and proportions of each of the sex and age categories recognizable in the field for each month of road strip sampling.

Month		Adult males		Adult and immature females		Immature males		Juveniles		Total
		No.	%	No.	%	No.	%	No.	%	
	1971	673	19,8	1 720	50,6	268	7,9	737	21,7	3 398
Jan	1972	656	22,0	1 380	46,3	194	6,5	751	25,2	2 981
	Total	1 329	20,8	3 100	48,6	462	7,2	1 488	23,3	6 379
	1970	483	16,8	1 516	52,7	213	7,4	664	23,1	2 876
Feb	1971	518	19,3	1 340	50,0	182	6,8	641	23,9	2 681
	Total	1 001	18,0	2 856	51,4	395	7,1	1 285	23,1	5 557
	1970	433	18,8	1 109	48,1	159	6,9	606	26,3	2 305
Mar	1971	528	20,5	1 231	47,9	202	7,9	608	23,6	2 571
	Total	961	19,7	2 340	48,0	361	7,4	1 214	24,9	4 876
	1970	428	17,6	1 291	53,1	175	7,2	537	22,1	2 431
Apr	1971	474	18,9	1 210	48,4	190	7,6	628	25,1	2 502
	Total	902	18,3	2 501	50,7	365	7,4	1 165	23,6	4 933
	1970	396	18,3	1 084	50,2	153	7,1	527	24,4	2 160
May	1971	380	18,5	1 058	51,6	151	7,4	462	22,5	2 051
	Total	776	18,4	2 142	50,9	304	7,2	989	23,5	4 211
	1970	348	17,0	949	46,3	156	7,6	596	29,1	2 049
Jun	1971	492	20,6	1 050	44,0	172	7,2	670	28,1	2 384
	Total	840	18,9	1 999	45,0	328	7,4	1 266	28,5	4 433
	1970	414	21,2	908	46,5	160	8,2	470	24,1	1 962
Jul	1971	560	24,8	940	41,7	197	8,7	557	24,7	2 254
	Total	974	23,2	1 848	43,9	357	8,5	1 027	24,4	4 206
	1970	390	22,6	791	45,9	143	8,3	400	23,2	1 724
Aug	1971	560	27,4	808	39,6	182	8,9	492	24,1	2 042
	Total	950	25,2	1 599	42,5	325	8,6	892	23,7	3 766
	1970	386	18,3	1 020	48,3	188	8,9	518	24,5	2 112
Sep	1971	442	21,5	916	44,5	194	9,4	507	24,6	2 059
	Total	828	19,9	1 936	46,4	382	9,2	1 025	24,6	4 171
	1970	431	19,2	1 334	59,4	243	10,8	238	10,6	2 246
Oct	1971	403	19,2	1 224	58,3	209	10,0	262	12,5	2 098
	Total	834	19,2	2 558	58,9	452	10,4	(4)500	11,5	4 344
	1970	694	27,6	1 535	61,0			286	11,4	2 515
Nov	1971	752	28,5	1 470	55,7	(3)		416	15,8	2 638
	Total	1 446	28,1	3 005	58,3			(4) 702	13,6	5 153
Dec	1970 (2)	882	30,7	1 752	61,0	236	8,2	(1)		2 870

Notes: (1) Number of juveniles not recorded as census carried out during peak of parturition.
(2) Only one count held – in December 1970.
(3) "Immature" (two year old) males indistinguishable from adults.
(4) Juvenile females indistinguishable from adults.

in greater detail in Chapter 12.

10.2.2. Waterhole counts.

Figures from counts at waterholes are not available for all months of the year as it was at times uneconomical, in terms of numbers of animals seen, to spend the necessary time at the waterholes. Very few animals in fact visited the waterholes during the summer months.

It was evident, however, both from the results obtained and from other casual observation, that some adult males tended to remain in the vicinity of water for hours on end, whilst herds of females and juveniles seldom stayed longer than was necessary for them to quench their thirst. Although those that did come stayed longer, comparatively few adult males visited water, so that this method was abondoned as a reliable means of obtaining data on sex ratios and age structure of impala.

The only sample of worthwhile size was obtained in March, 1970, when a total of 1 987 animals was sampled during the course of two consecutive days at the two main waterholes. The proportions of the recognizable catagories that were recorded were as follows:

Adult males	18,4%
Adult females	44,6%
Immature males	8,6%
Juvenile males	10,7%
Juvenile females	17,7%

These proportions, together with the sex ratios of 60 : 100 (1 : 1,66) for adults and immatures and 61 : 100 (1 : 1,65) for juveniles, closely resemble those obtained from the road strip sample.

10.2.3. Jaw material.

It was mentioned earlier in this chapter that, after the age of about nine months in females and two years in males, it was very difficult to distinguish the age catagories in the field. For this reason, there is assumed to be no bias towards any particular age group in the shooting records of males after two years of age, and it is reasonable to conclude that the age ratio in which the sample was collected represents the ratio in which the animals occurred in the population. It is therefore valid to use the data so obtained in the construction of a life table for males along the lines of "Case 3" of Deevey (1947 : p. 288), in which "... the age structure is obtained from a sample, assumed to be a random sample of the population...".

The sample used in the construction of the female life table was derived exclusively from animals that either injured themselves in capture and were destroyed, or that died as a result of stress imposed by the capture. It included a number of animals from Nxwala State Land where some of the capture took place.

At the same time a sample of animals that had died from natural causes was also obtained (see Chapter 11), enabling data for the construction of life tables to be obtained by a second method, "Case 1" of Deevey (1947).

For the purpose of further analysis, a situation generally known as a "stable age distribution" is assumed. This assumption is made on the grounds that the age distributions derived from the ageing techniques based on the height of the first molar for 1971 and 1972 were very similar. Furthermore, the relative proportions of the various categories recognizable in the field were not significantly different between the two years in which the samples were obtained (see Table 38). This evidence supports the assumption that the age distribution was stable, at least for the study population during the study period.

The age structure of the largest two-monthly samples of males (February/March 1971) and females (August and September 1970), aged by the method described in Chapter 8.3.5., is shown in Table 39. Because of the bias against the shooting of younger animals the numbers of juvenile males and females and immature males used in the table have been calculated from other available data. The methods whereby this has been done are shown beneath the table, together with necessary information on the proportions of the age and sex categories recognizable in the field. The juvenile sex ratios have been obtained from data given in Table 37. For August/September 1970, this is 1 : 1,7 and for February/March 1971, it is assumed to be 1 : 1,40 since the ratio in April, when it was first possible to sex juveniles, is 1 : 1,38, which is not significantly different from the foetal sex ratio given in Chapter 9.5.2.

Two or three years earlier, in July 1968, the juvenile sex ratio showed a preponderance of males: 1 : 0,78 (University of Natal Wildlife Society 1968). These results

Table 39. Age distributions of Mkuzi impala, using samples culled in August/September 1970 (227 females) and February/March 1971 (99 males). Calculations of the relative numbers of juveniles and of immature males are shown.

Age	Frequency	
	Females	Males
0–1	73^{x}	50^{z}
1–2	51	37^{y}
2–3	33	29
3–4	25	16
4–5	22	12
5–6	21	11
6–7	20	10
7–8	17	7
8–9	16	5
9–10	13	3
10–11	8	3
11–12	1	2
12+	–	1
Total	300	186

Proportions of field recognizable categories:	Aug/Sep	Feb/Mar
Adult males	20,2%	19,8%
Immature males	8,6%	7,4%
Adult females / Immature females	47,2%	49,0%
Juvenile males	8,7%	23,9%
Juvenile females	15,2%	

By proportion:

$$a\frac{x}{227} = \frac{15,2}{47,2} \qquad x = 73$$

$$b\frac{y}{99} = \frac{7,4}{19,8} \qquad y = 37$$

$$c\frac{z}{136} = \frac{9,9}{27,2} \qquad z = 50$$

where a = number of females over one year (adult + immature)
b = number of males over two years (adult)
and c = number of males over one year (adult + immature).

are in marked contrast to the findings in the present study, and may be a result of inadequate sampling (n = 787).

CHAPTER 11.

MORTALITY

11.1. General.

Before it is possible to construct and discuss life tables, some analysis of mortality rates and factors is necessary. A summary of data on the mortality of impala in Mkuzi is shown graphically in Figure 37. These data are derived from carcasses no more than a week or two old which were found only incidentally, and not as a result of any concerted effort. Despite this, very good coverage of the area was obtained because of the nature of the administrative activities by the staff. Where any doubt existed in the mind of the observer, the cause of death was recorded as unknown (C.O.D.U.).

Since none of the data represent the outcome of any special effort to seek carcasses, it is assumed that the sample of recorded natural deaths was a random one with respect to frequency in each month, as well as to age structure. The mortality of adult males showed a marked peak in midwinter, followed by a trough in August and another peak in October. The first peak can be explained by the fact that the condition of males after the rut was low, and the state of the habitat in winter placed an increased stress on these animals.

Child (1968) mentions that the mortality of adult males

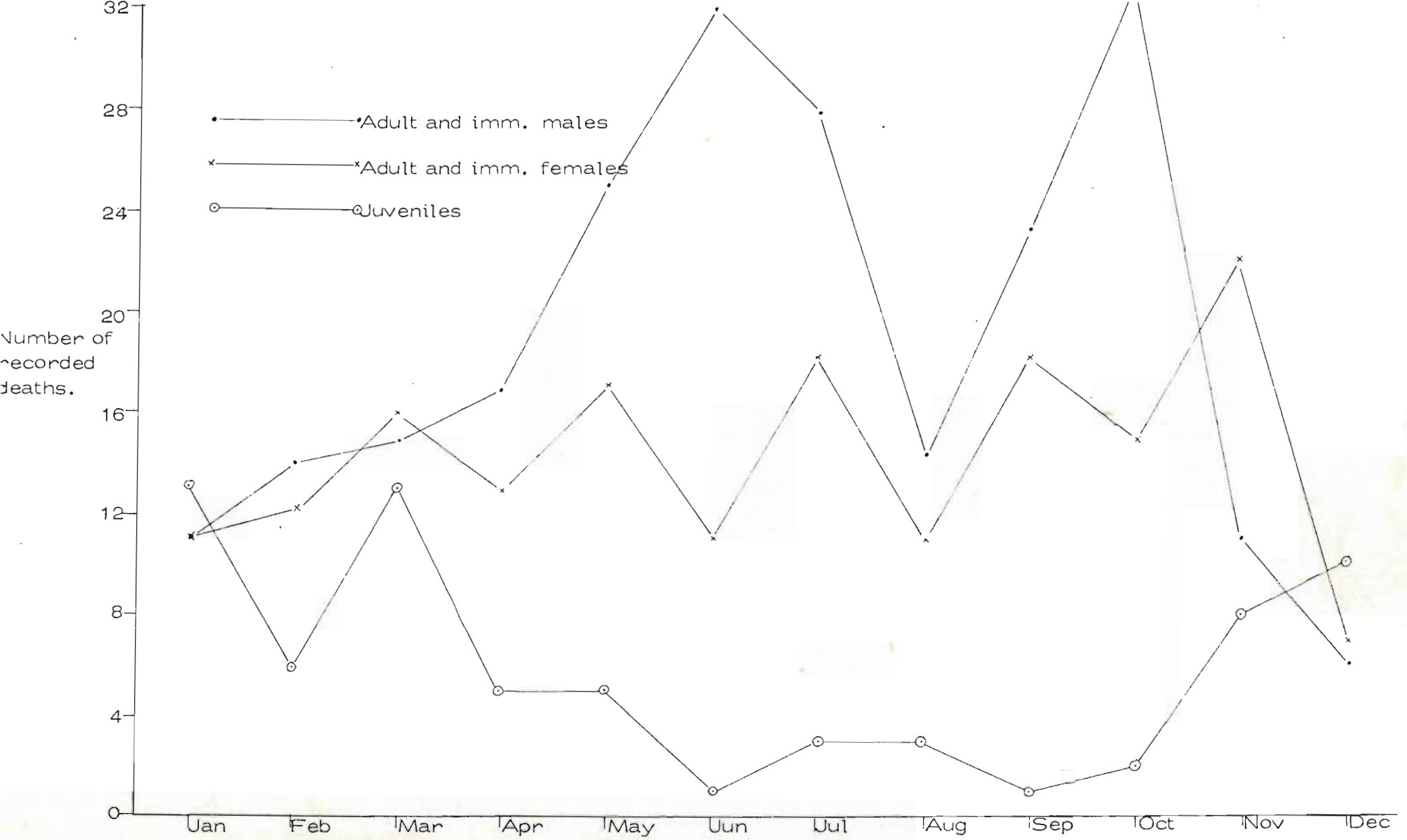

Figure 37. Frequency of recorded natural mortalities of impala for each month in 1970 and 1971. The data for the two years have been combined.

immediately after the rut is very heavy, especially in critical years, and attributes this to the fact that they are in poor condition at this time. The reason for this poor condition is probably the stress imposed by territorial behaviour.

Anderson (1965) reported a minimal kidney fat mass (which is generally regarded as an index of condition (Riney 1954)) in July in a nearby area, thus providing quantitative evidence for the contention that the condition was low in winter following the rut. The recorded drop in mortality in August has no apparent explanation, unless it was that most of those males in poor condition succumbed before this time, and the subsequent rise in October was due to animals that suffered as a result of the dry season.

Female mortality was recorded at a more or less constant rate throughout the year, with only one peak in November, coinciding with the approach of parturition. Again increased stress, due in this case to the drain on the reserves of the dam during pregnancy, probably accounted for this increase of mortality rate. Eight of the 24 females (33%) recorded as dying in November were more than eight years of age, compared to the 13% represented by this group in the population.

Juveniles had a comparatively high rate of mortality during the first four months of life (December to March), when 73% of the deaths of animals in their first year were recorded. A further 14% occurred in the next two months, whereas during the late winter months the mortality rate of juveniles was very low. It was perhaps to be expected

that juvenile mortality was under-represented in the recorded sample because of the greater fragility of the remains. Spinage (1972) arbitrarily set the mortality rate for impala in their first year in Rwanda at 50%, whilst Jarvis and Morris (1960) reported that the rate of mortality of juvenile impala was just 50% in captivity. This question will be discussed in greater detail in Chapter 12.

11.2. Causes of mortality.

The causes of death of impala in Mkuzi can be placed in several categories, described by Dasmann (1966). These are:

11.2.1. Predation.

Predation on the study population was fairly high, and those species recorded as preying on impala in Mkuzi during the study period were: cheetah, jackal, python (Python sebae), hyaena (Crocuta crocuta), crocodile (Crocodilus niloticus), and eagle. Predation as a cause of death was recorded as such only when there was no doubt in the mind of the observer as to the identity of the predator species, so that many of the deaths recorded as "C.O.D.U." could well have been added to the data. The various predators were responsible for the following impala deaths between February 1970 and January 1973:

Cheetah	37
Jackal	40
Python	8
Hyaena	2
Crocodile	1
Eagle	1

A total of 89 out of 498 (17,9%) deaths recorded in three years was therefore attributed directly to predation. A further two animals were recorded as having died of snake bite.

Out of 37 cheetah kills, 17 were adult male impala, 17 adult female, and only three juvenile. Comparable figures for jackal were 10, 14 and 16 respectively. All the known-age python kills were of juveniles; only five were aged, while the remaining three had been consumed so far as not to allow identification of the age or sex of the victim.

These figures may be compared with those provided by Pienaar (1969) for Kruger National Park, who found that about 16% of the impala recorded as prey of cheetah were juveniles in their first six months of life. Pienaar also recorded a sex ratio of impala in cheetah kills of 30% males and 60% females (10% unsexed), whilst in Mkuzi the ratio was 46% : 46% (8% unsexed juveniles).

No comparable figures for jackal kills in Kruger National Park are available. The sex ratio of adult kills in Mkuzi was not significantly different from the mean sex ratio determined for the population, so that it is concluded that there was no bias in the choice of sexes by jackal. In the case of adults it was apparent from the records that a

high proportion of the adults killed by jackal were old, sick, or lame individuals. The proportion of juveniles in the jackal kill, however, was significantly higher than it was in the population - 40% in the kill as against only 25% in the population (chi square = 70,6, d.f. = 1, $P < 0,005$) suggesting that there was a bias towards juveniles. One recorded jackal kill was of a female giving birth.

No seasonal changes were apparent in the pattern of predation by either of the two major predators of impala in Mkuzi, except for the expected rise in predation on juveniles (by jackal in particular) between November and March, coinciding with the peak of all mortalities in this age group.

The single record of predation by an eagle was by the martial eagle (Polemaetus bellicosus), in November, when the bird was feeding young. Remains of impala were also evident in the vicinity of the nest.

11.2.2. Diseases and parasites.

No specific study of the zoonoses affecting impala in Mkuzi Game Reserve has been carried out, but doubtless many of the animals recorded as "C.O.D.U." succumbed to one or another of these factors. In those few of the carcasses upon which field post mortems were carried out a high proportion had symptoms of pneumonia and/or lesions of the liver (M.E. Keep, pers. comm.).

It is never easy to diagnose death due to parasitic infection, but a few animals that were seen still alive,

but in poor condition, were heavily infected with sarcoptic mange, with every likelihood of their dying as a result. This may have been a secondary condition linked to debility caused by some other factor such as a primary disease or undernutrition.

11.2.3. Accidents.

Several kinds of accident befell impala during the three years of the study, but only one could be thought of as having any real effect on the population - and then only very slight. This was entanglement in the fence that separates the game reserve from Nxwala State Land. Normally, impala find this fence no barrier to movement, but they do occasionally have mishaps. On the other hand, because the fence was regularly patrolled, nearly all the fatalities from this cause were located, so that the observed number of 17 mortalities from this cause in three years was rather biased.

Only two of probably a good deal more impala were recorded as having died as a direct result of being struck by vehicles. It is likely that many such deaths go unrecorded, for animals frequently get demaged and may later die or be killed by predators.

There are three records in three years of impala being destroyed because of broken limbs and similar injuries. It is not unlikely that such individuals would in any event have fallen easy victim to predators, although destruction by human agency because of this is not strictly speaking a recognised mortality factor.

11.2.4. Weather.

In the late winter of 1966, the situation became extremely serious when the source of water for the artificial waterholes failed as a result of drought. Large numbers of animals died and many others emigrated in search of water. This drought in fact had a very profound effect upon the Mkuzi impala population, for it was some years before it recovered again to anything resembling its level prior to 1966. In fact it was probably still affected by this disaster at the time of the study.

Otherwise it is doubtful whether the weather in Mkuzi exerts any direct influence on the population by causing mortality. For instance, during the study period temperatures never reached such levels that death from exposure alone would have resulted. The combination of poor condition and low temperatures experienced during the passing of regular "cold fronts" may well be a significant factor in mortality, however. One cause of death which may be attributable directly to weather is lightning, but no cases of impala being killed in this way have been recorded.

One death in 1971 was attributed to "dehydration", which was indirectly caused by the weather. It occurred during a prolonged dry spell which coincided with a breakdown of the pumps supplying the artificial waterholes. There was, therefore, no surface water in the reserve for a short spell.

The cause of death of one animal in the course of the three years of the study was quoted as being "stuck in mud". This occurred at a seasonal waterhole in the final stages of its drying up.

11.2.5. Hunting.

Whilst hunting by man was once to be recognised as a form of predation, the sophistication of weapons today and the pressure on the limited wildlife resource as a source of meat precludes subsistence hunting as a means of naturally controlling or regulating numbers. Hunting in Mkuzi takes two forms: illegal hunting or poaching, and population reduction as a means of management. The latter was carried out by shooting or live capture, and it was in the course of shooting that material became available for much of the study reported here.

Unlike the deaths caused by animals being caught up in the fence, it is estimated that only a very small proportion of the deaths caused by poaching was discovered. The main poaching technique employed in Mkuzi Game Reserve is snaring with wire nooses, and during the three study years 44 impala were found snared, as against only two known to have been killed by poachers' dogs. Many other cases doubtless went undetected, and the actual numbers will probably never be known.

"Legal hunting" or population reduction, accounted for a known number of removals from the population. Those animals that were caught alive and distributed were to all

intents and purposes also deaths for their effective role in the Mkuzi population ceased at the time of capture. The removal figures for the three years were as follows:

Year	Shot	Captured	Total
1970	288	1 374	1 662
1971	449	2 148	2 537
1972	259	3 084	3 343

The increased rate of removal each year was necessitated by the lack of knowledge of the dynamics of the population and by the fact that, until a better knowledge thereof had been obtained, the number to be removed annually was arrived at rather arbitrarily. As a consequence the tendency was to be on the conservative side, and it was found that the habitat continued to deteriorate despite the removal. Management, although becoming more refined all the time, will continue to be the subject of some degree of guesswork until it is possible to assess carrying capacity in a completely objective fashion.

11.2.6. Behavioural factors.

Into this category have been placed a number of factors which are inherent in the population or in the impala themselves, and which are not due to any environmental influence whatsoever.

A mortality factor emanating from territorial behaviour in males was intraspecific fighting. Despite the fact that, generally speaking, encounters with individuals of the same species and sex have evolved into ritualised patterns of behaviour in most animals, serious contests do still take place. This is also true of impala. Fourteen such fatalities were recorded

in three years. All victims were adult males, and the peak period for deaths from this cause (April to June) coincided with the period of the rut and the peak of territorial behaviour, when fighting itself was most frequently observed.

Two animals were recorded as having died whilst giving birth, and were found in a state of partial parturition, with both dam and foetus dead. (A third female, as was mentioned earlier, was killed by jackal whilst giving birth). Two lambs were recorded as stillborn. This must represent a comparatively small proportion of such cases for scavengers, particularly at the time of parturition, are very active, and any stillborn young would not remain undetected for long.

A most critical period for both juveniles and their mothers was during parturition, when the females left the herds and went off on their own or in small groups, and when the young were comparatively helpless. The physiological stress on females at this time was also considerable, particularly in the case of older animals.

The lambs which were born early, before the main breeding season, would also probably be more vulnerable to predation, although it was not possible to prove this.

CHAPTER 12

LIFE TABLES

12.1. Introduction.

A life table is essentially a means of presenting data of population survival and mortality in concise form. The technique of constructing such a table has been in use for a long time, not only in wildlife studies, but also for human demographic and actuarial purposes.

There are two basic forms of life table, the first being the "dynamic" and the other the "time-specific" life table. The former depends upon a single year's cohort of animals being followed throughout their lives and the age at death being recorded in each case. The time-specific life table is that wherein the mortality or survival of each age class in a given population is recorded over a short period, thus describing the current status of the population.

The possibility of constructing a dynamic life table for larger mammals in the wild is remote, for few if any studies, other than those of man, have been carried out. Such a study would involve a good deal of time, tracing the course of life from birth to death of each individual of a sample of animals from a population. Comfort (1957) was able to do this for a number of species of large mammals that hed been bred in captivity and kept in zoos, whilst life tables have been constructed in this way for numerous species of birds and small mammals.

Deevey (1947) described three groups of basic data that may be used for the construction of life tables: 1) The age at death is recorded for a large and random sample of the population. 2) The survival of a large cohort born at the same time is followed at intervals through its exixtence. 3) The age structure is obtained from a sample - assumedly random - and the rate of death is inferred from a shrinkage between successive age classes. Other means of obtaining data for the construction of life tables have been listed by Caughley (1977). A prerequisite for all these methods is to assume a stable age distribution if the life table is to be used for retrospective and predictive projections. This is a situation wherein the age structure of a population does not change from year to year, so that the various population parameters derived from the life table are constant with time.

Caughley (1966) rightly pointed out that the second method of Deevey (1947) for the construction of a life table, is generally useful only for studies on small mammals. He also added that such a table is valid only under stable age distribution conditions.

In the present study, method 3 of Deevey (1947) was the most reliable method of obtaining data, because of the size of the sample, although a sample whose age at death was known was also obtained and a life table constructed from these data as described in method 1.

12.2. Life table from l_x data.

It was earlier mentioned (Chapter 8.3.5) how very

similar the age distributions of the collected samples of Mkuzi impala were in 1970 and 1971. It was for this reason that the impala population in Mkuzi Game Reserve was assumed to have a stable age distribution, at least for the period of the study. The data obtained were therefore sufficient to construct a time-specific life table for the Mkuzi population in 1970 and 1971 by the third method of Deevey (1947). It is not possible to refer to a life table that has been constructed from data obtained from one population as being representative of the species as a whole. A species is subjected to all sorts of different environmental conditions in various parts of its range, so that mortality, to mention but one factor, is quite different between one population and another. Furthermore conditions change from year to year in the same area. Thus the life tables which follow are not only time-specific to the period of the study, but are also applicable only to the Mkuzi population.

In order to construct as nearly as possible a time-specific life table for the Mkuzi impala population, sub-samples of 99 males and 227 females were extracted from the material. These sub-samples represented the largest samples that were obtained over a short period during the course of the study. In the case of males the animals shot in February and March 1971 were used; and in the case of females, those that died as a result of capture in late August and early September 1970 were used.

It is possible that older animals may have been more susceptible to death due to stress from capture, but since only 33 animals in the last four age classes (12,3% of the

sample) were obtained, any bias due to this factor would have been small.

Deevey's (1947) third method for obtaining data for the construction of a life table is also known as an l_x series. It is based on a measurement of the rate of survival, as opposed to that of the rate of mortality, the latter being known as a d_x series. Life tables derived in the former fashion are shown in Tables 40 and 41, for males and females respectively.

However, because the youngest age classes of both sexes are under-represented in the samples, and because the samples were not obtained at the period of parturition (late November and early December) it has been necessary to extrapolate for the purpose of deriving some of the data. In order to do this, survival curves were drawn using the data of Table 39, in which the numbers of juveniles and yearlings relative to the remaining age groups have been calculated. These figures refer to three month-old males and nine month-old females and survival was calculated from these data and plotted against age in months. The curves were continued back to zero months and the number of newborn obtained in this way, as shown in Figure 38. As a check, the first few points were also plotted on a logarithmic scale of numbers against age, because the survival closely resembles a reverse exponential curve for the first three years. The intercept on the y-axis confirms the earlier extrapolation.

In order to correct for true intervals of one year the frequencies were read off the intercepts of the log slopes at one and two years of age and these figures were used in

Table 40. Life table for male impala derived from a sample of 99 animals over two years of age obtained in February/March 1971, and aged by the molar wear wear method (see Table 29). The frequencies of the younger age classes are obtained by the method described in the text.

Age x	Frequency f	Survival 1 000l_x	Mortality 1 000d_x	Mortality rate 1 000q_x	Survival rate 1 000p_x	T_x	Life expectancy e_x
0	54	1 000	259	259	871	3 227	3,23
1	40	741	204	275	639	2 356	3,18
2	29	537	167	311	454	1 717	3,20
3	20	370	111	300	315	1 263	3,41
4	14	259	55	212	232	948	3,66
5	11	204	19	93	195	716	3,51
6	10	185	37	200	167	521	2,82
7	8	148	55	372	121	354	2,39
8	5	93	37	398	75	233	2,51
9	3	56	0	0	56	158	2,82
10	3	56	19	339	47	102	1,82
11	2	37	0	0	37	55	1,49
12	2	37	37	1 000	18	18	0,49

Table 41. Life table for female impala derived from a sample of 227 animals over one year of age obtained in August/September 1970 and aged by the molar wear method (see Table 31). The frequencies of the younger age classes are obtained by the method described in the text. All yearlings and some two year olds were aged by tooth replacement.

Age x	Frequency f	Survival $1\,000l_x$	Mortality $1\,000d_x$	Mortality rate $1\,000q_x$	Survival rate $1\,000p_x$	T_x	Life expectancy e_x
0	95	1 000	306	306	653	3 214	3,21
1	66	694	252	363	568	2 561	3,69
2	42	442	126	285	379	1 993	4,51
3	30	316	53	168	290	1 614	5,11
4	25	263	31	118	248	1 324	5,03
5	22	232	11	47	227	1 076	4,64
6	21	221	21	95	211	849	3,84
7	19	200	21	105	190	638	3,19
8	17	179	21	117	169	448	2,50
9	15	158	32	203	142	279	1,77
10	12	126	52	413	100	137	1,09
11	7	74	74	1 000	37	37	0,50

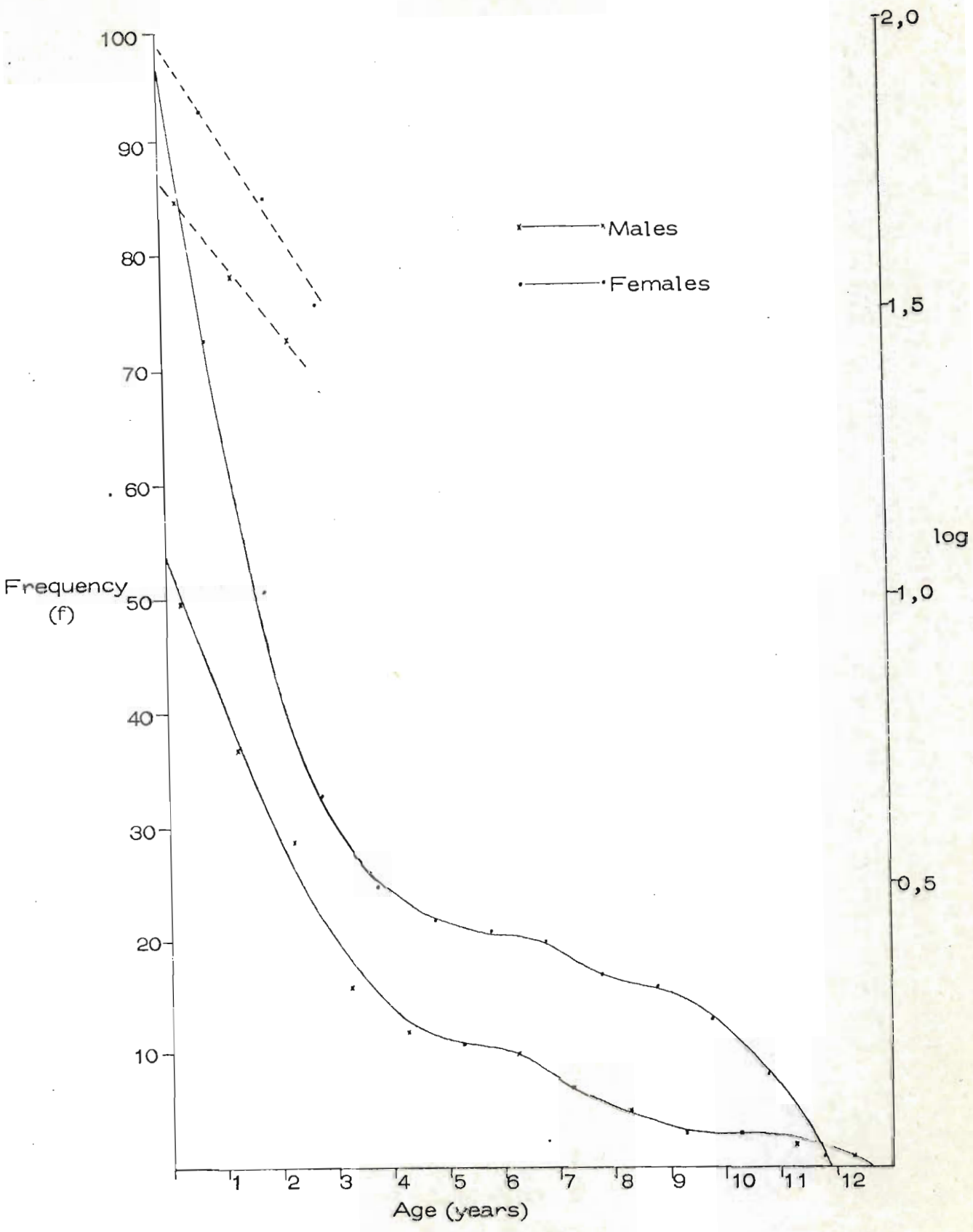

Figure 38. Survival of the sample of impala and the log of the survival, plotted separately against age. See text for details.

the construction of the life tables. From three years onwards actual data were used, although the samples were not taken at time of birth of young. In the case of females the frequency in the one year olds was 51 by the direct method and 66 by the indirect method; for males it was 37 and 41 respectively. At two years old these frequencies were 33 against 46 for females, and 29 against 30 for males.

The standard notation for life tables has been used in Tables 40 and 41, and the various parameters are:

l_x = the number surviving at the start of the age interval out of a cohort, in this case of 1 000. It is also the probability at birth of an individual surviving to age x.

d_x = the relative proportions dying in the age interval x, x+1. It is calculated as $l_x - l_{x+1}$.

q_x = the rate of mortality in the age interval x, x+1, calculated by d_x/l_x. Also the age specific mortality between x and x+1.

p_x = the mean number surviving in the age interval x, x+1, calculated by $(l_x + l_{x+1})/2$.

T_x = total frequency of live animals at the start of each age interval.

e_x = life expectancy at age x, the start of the age interval.

These life tables may be compared with those of Spinage (1972) which are in fact d_x series, having been derived from data obtained from material collected after death from natural causes in the field. Spinage did, however, make two

assumptions in deriving his life tables, one of which was that the mortality rate in the first year of life was 50%. No evidence was provided for this assumption. However, data extrapolated from the Mkuzi life tables allow an estimate of juvenile mortality to be made for this population. Directly evident from Tables 40 and 41 is that male mortality in the first year is 24,1% and for females it is 30,5%.

In comparison with the estimates by Spinage (1972) of 50% juvenile mortality, these figures are considered to be fair, because of the comparatively light predation pressure which exists in Mkuzi, and the possibility that the population was still increasing after the crash in 1966.

Several graphic illustrations of the demographic features evident from the l_x life tables will help to make these features clearer. The rate of mortality ($1\,000q_x$) is shown in Figure 39 for both sexes; the data have been smoothed by the use of polynomials (Snedecor 1956: p. 461), and the actual life table figure for the rate of mortality of males in the first year has been included and linked to the smoothed curve by a dotted line.

In Figure 40 the survival rate ($1\,000p_x$) is plotted against age for both sexes, using the data smoothed by polynomials. Finally, as a means of comparison with the data of Spinage (1972), the logarithmic survival curves ($\log 1\,000l_x$) have been drawn in Figuré 41; these curves have not been smoothed.

The parameter q_x, the rate of mortality or age specific

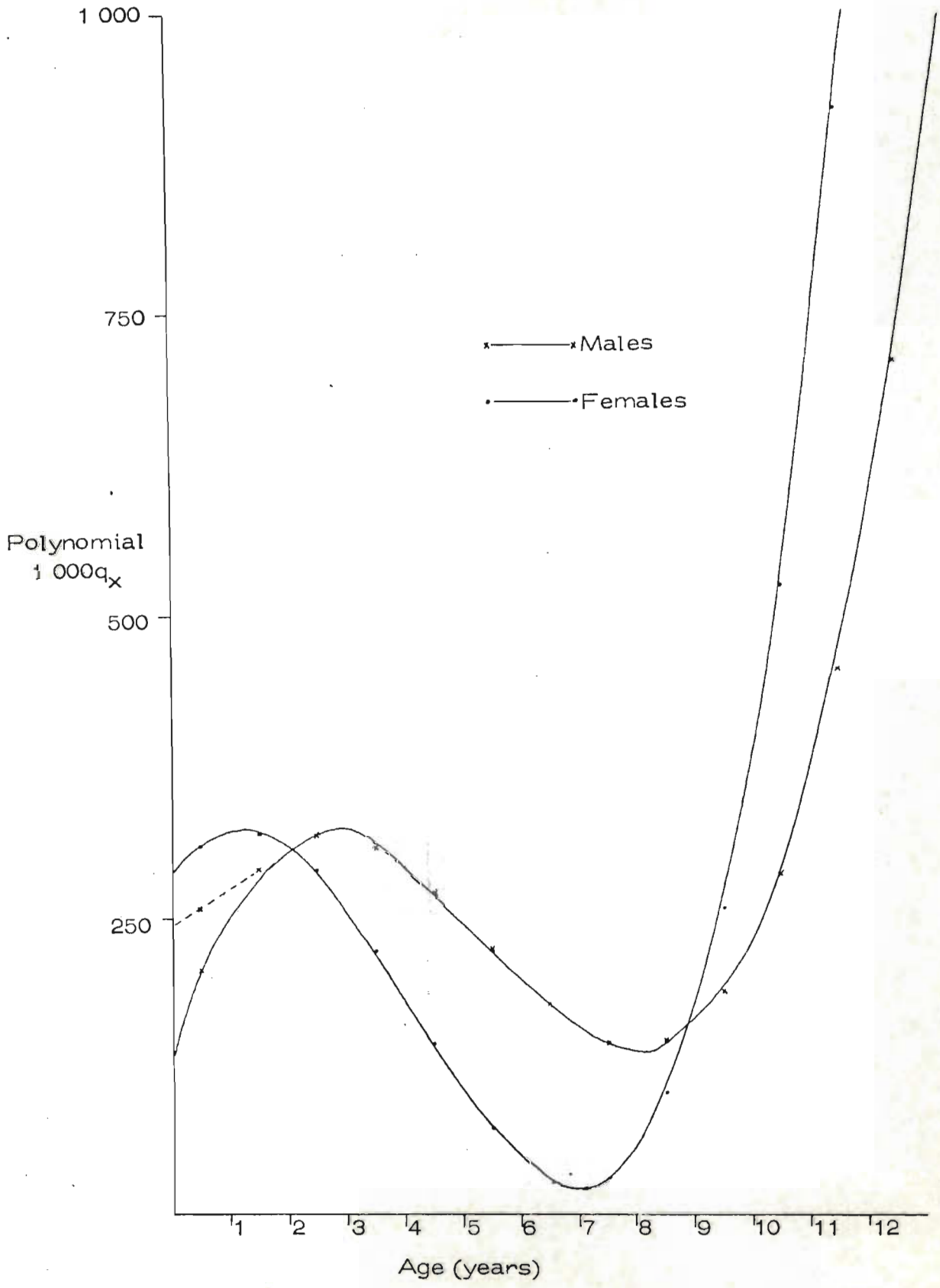

Figure 39. Polynomial plot of rate of mortality (1 000q_x) data derived from l_x life tables.

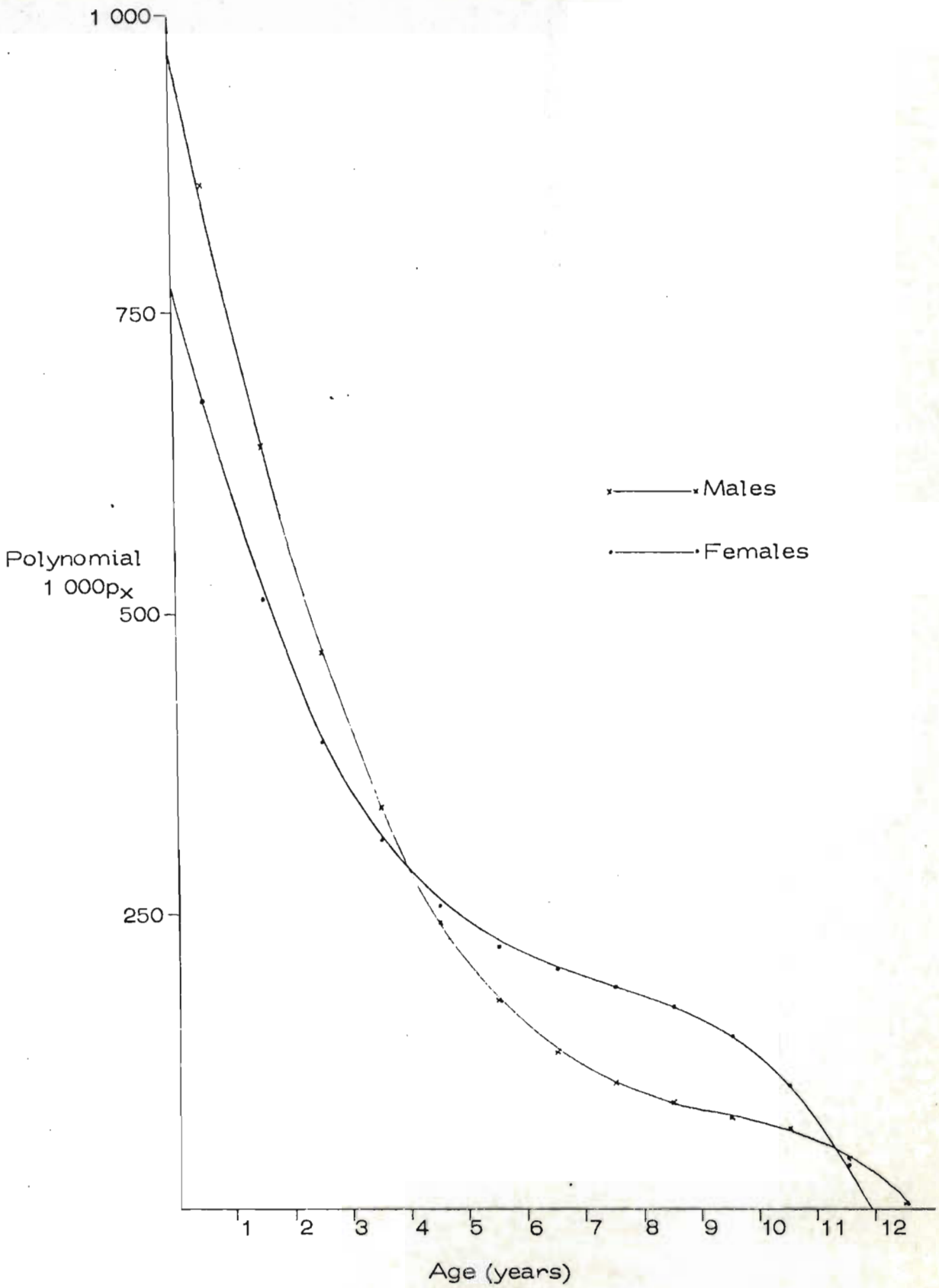

Figure 40. Polynomial plot of the survival rate (1 000p_x) data derived from the l_x life tables.

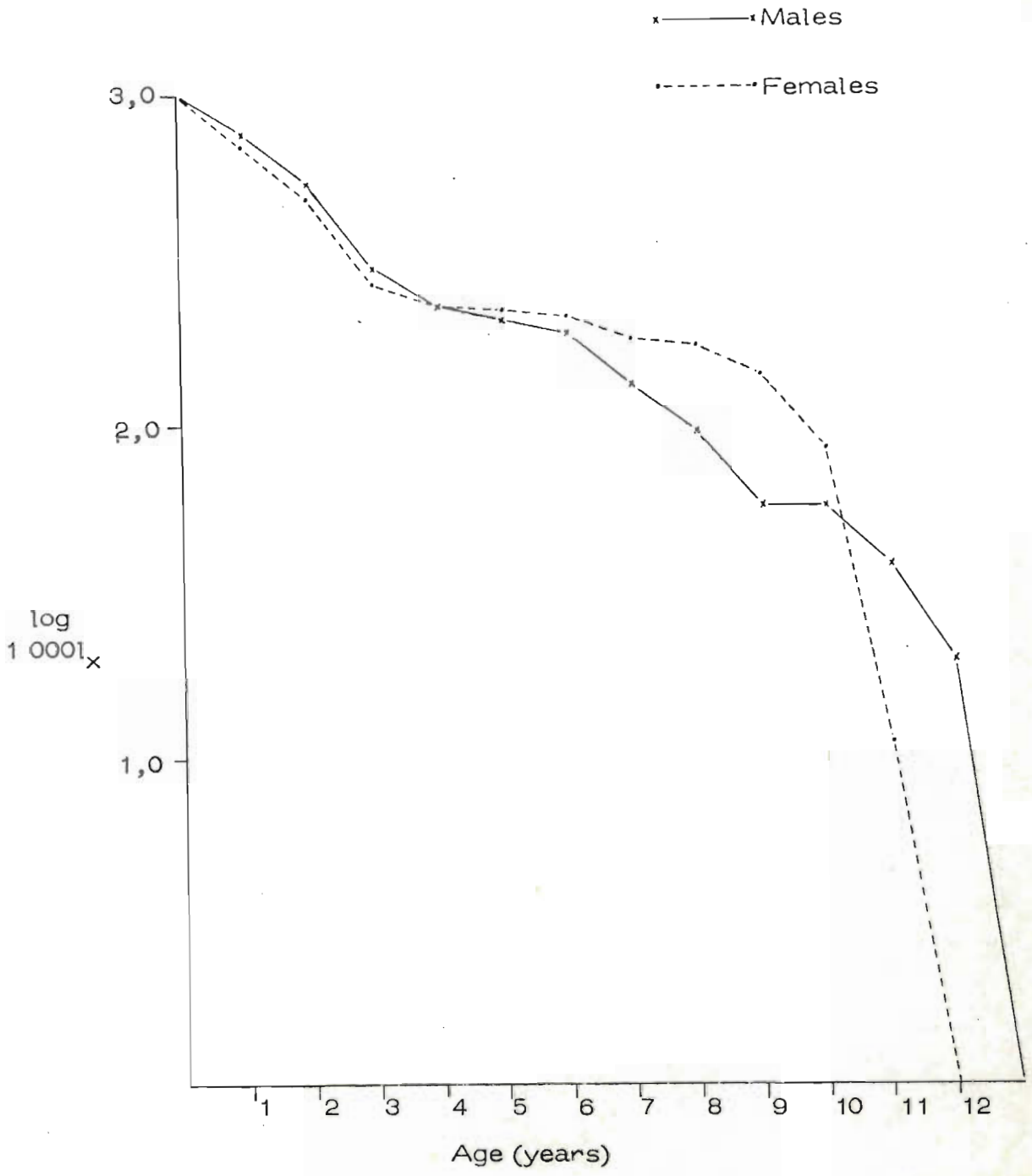

Figure 41. Survival curves (log 1 0001_x) of impala, based on data from l_x life tables.

mortality, is the one least affected by sampling error. By the way in which a life table is calculated, any error in the younger age classes is carried through the table in p_x and l_x to the end, whereas q_x is independent of all but the frequencies at ages x and x+1. Thus it is the best way by which populations may be compared in their demographic behaviour.

12.3. Rate of increase.

Caughley (1977) has summarised the relationships between the rate of increase of a population and the various demographic parameters. Amongst other things he points out that it is not possible to derive the rate of increase from the data provided in a life table which is obtained either from the ages at death of a sample of individuals, or from the age distribution of a single sample of animals alive at a given time, i.e. from a d_x or l_x series.

The reason for this is that a temporal age distribution of a single cohort of animals is the same as the standing (time-specific) age distribution, only if the rate of increase is zero. Time specific life tables, such as were presented in Section 12.2 (Tables 40 and 41), illustrate only single age distributions, and cannot therefore be used to calculate a rate of increase by the usual method described by Caughley (1977). An age distribution s_x is expressed as the number of animals in age class x relative to the number of newborn, whilst the survival l_x is obtained by dividing the number represented in the sample in age class x by the number in class 0 (newborn). Thus l_x and s_x for a time-specific age distribution are the same, and since $r = \frac{\log_e l_x - \log_e s_x}{x}$, r, the rate of increase, must be zero.

In order to calculate the population rate of increase, comparisons were made between the populations in 1970 and 1971, estimated by road strip sampling (Tables 10 and 11). When individual months are considered, the rate of increase varies from -4,7% in May to 9,7% in September; some of the variation can be attributed to sampling error, but some is also caused by the major capture operations. In 1970, 1 353 animals were removed by capture between the August and September counts, so that if these are added back into the September figure, the increase is only 0,3%. Similarly in 1971, 2 148 were removed between the May and June counts and if they are added to the June count the rate of increase becomes 19%.

The difference between the mean estimated population in 1970 and 1971 is 598, or 3,5% increase from 1970 to 1971. This figure takes into account the number of animals removed in the two years.

Another method was used to estimate the rate of increase; this was based on data from the l_x life table. A model was constructed in which 16 successive generations (or any number of generations as long as it is more than the life span of 12 or 13 years) were traced, using the demographic parameters derived for the Mkuzi population. Survival rates were obtained from the l_x life table, fecundity rates were those described in Chapter 9.4.1; and the sex ratio at birth was taken as 1 : 1,4 (see Chapter 9.5.2).

Such a model is shown in Figure 42, from which the rate

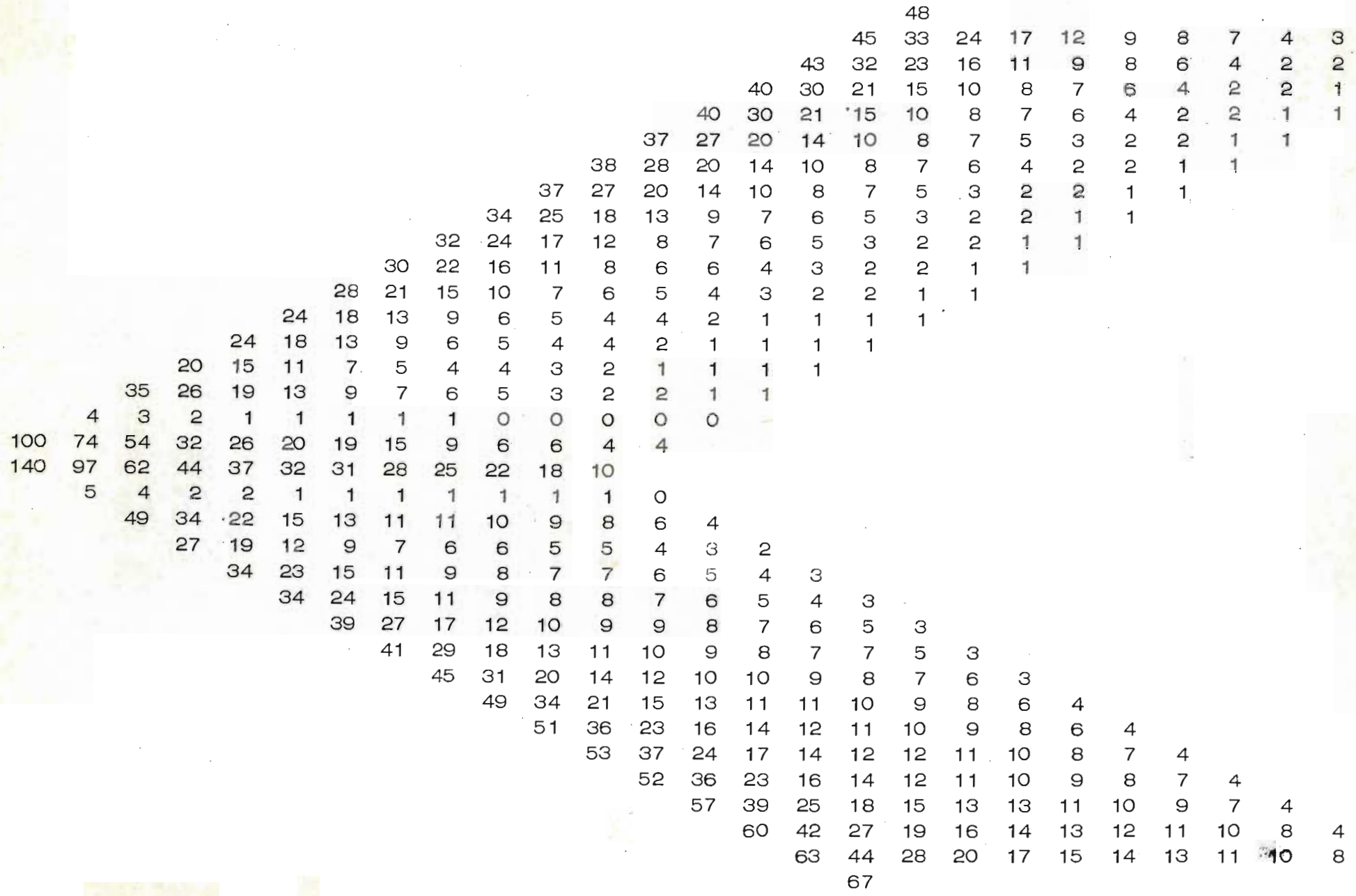

Figure 42. Population growth model using the data from the l_x life tables.

of increase between successive years of the model is calculated as 4,65%. In exponential form $e^{rx} = 1,0475$ and $r_x = 0,047$. For males the figure is 4,70% ($e^{rx} = 1,0480$ and $r_x = 0,047$) and for females 4,62% ($e^{rx} = 1,047$ and $r_x = 0,0460$).

This method provides a "time-specific" instantaneous rate of increase under the demographic conditions pertaining at the time. It enables comparisons to be made from year to year and, because it is determined from the age distribution, the rate of increase can be predicted and used for management purposes.

The rate of increase of 4,65% calculated in this way is similar to the 3,5% increase obtained by comparing total populations between the two successive years of counting.

The incremental rate for the addition of the various age groups to the population can also be calculated. Thus, in the sixteenth year of the model newborn animals comprise 29,3% of the population which is 70,5 lambs per 100 females. However, incremental rate is more commonly expressed in terms of the addition of breeding animals to the population. In the case of yearlings (some of which are at breeding age), the rate is 38,5%, and in the case of two year-old animals (most of which breed), it is 34,6%. Put in other terms, yearlings comprise 27,9% of the animals one year and older and two year-old animals make up 25,7% of the entire population over two years old.

12.4. Life table from d_x data.

A life table of Deevey's (1947) first type, based on the ages at death of a sample, is known as a d_x series. Over the two year period, 1970 to 1971, a total of 480 deaths was recorded. Of these 413 animals were older than one year and 67 were juveniles. Because of the state of the remains it was possible to sex 391 animals over one year old and of these 220 were males and 171 females. In the case of the remaining 22 carcasses either the mandibles were absent or it was not possible to sex them because the skull could not be found.

Several authors (Woodgerd 1964, Caughley 1966, Spinage 1972) have pointed out that there is a distinct bias against finding skeletal remains or carcasses of young animals because of their greater fragility and because they are more easily consumed in toto by scavengers. Mortality figures for juveniles must therefore be treated with caution and those recorded in this study have not been used in the construction of a d_x table.

The sex ratio of animals over one year of age which were found dead was 1 : 0,78. The sample sex ratio of animals over one year old in the standing population was 1 : 0,70, so that there was a higher proportionate mortality of males in these age classes. Spinage (1972) considered that the reason why more male deaths were recorded may have been the greater difficulty with which scavengers were able to dispose of the remains. However there is unlikely to be any difference in the disposability of the mandibles of males and females, upon which ageing is based, and this factor is therefore not considered to be important.

Separate life tables for males and females have been constructed from the data obtained from the age structure of animals found dead in the field from "natural" causes. These are presented in Tables 42 and 43 respectively. For lack of more accurate data, mortality frequencies of animals in their first year of life were drawn from Tables 40 and 41, and adapted to the respective frequencies of animals found dead.

Because a prerequisite for the construction of life tables from ages at death is a known rate of increase, it was necessary to apply a correction factor as described by Caughley (1977), based on the rates of increase derived from Figure 42, namely 4,70% for males and 4,62% for females. The correction factor is the exponential function of the rate of increase, e^{rx}. The observed frequencies are multiplied in each case by this factor to obtain the corrected frquency, and the mortality d_x, survival l_x, and mortality rate q_x entered into the life table.

The mortality rates have been plotted, after smoothing by means of polynomials, in Figure 43, for comparison with the smoothed curve of Spinage (1972) for male mortality rate. Instead of using actual ages in the abscissa, Spinage used the age as a percentage of the maximum life span. This appears to be a combination of methods based partly on that of Deevey (1947) in which the percentage deviation of the age from the mean length of life was used. Caughley (1966) critcised this method for the shape of the resulting curve depends to a large extent on the mortality rate in younger age classes. As has been shown, this is not easy to determine so that Deevey's method has limitations in the sort of study which can be

Table 42. Life table for male impala in Mkuzi Game Reserve in 1970–71, derived from mortality data and ages at death of 220 animals older than one year at time of death. See text for details.

Age x	f_x	Correction factor $e^{rx}(r=0,047)$	Corrected frequency fx^{erx}	1 000d_x	1 000l_x	1 000q_x
0 – 1	71*	1,000	71	194	1 000	194
1 – 2	11	1,047	11,5	31	806	38
2 – 3	23	1,099	25,3	69	775	89
3 – 4	16	1,151	18,4	50	706	71
4 – 5	15	1,207	18,1	50	656	76
5 – 6	29	1,265	36,7	100	606	165
6 – 7	23	1,326	30,5	83	506	164
7 – 8	24	1,390	33,4	91	423	215
8 – 9	28	1,456	40,8	112	332	337
9 – 10	32	1,527	48,9	134	220	609
10 – 11	12	1,600	19,2	53	86	616
11 – 12	5	1,677	8,4	23	33	697
12+	2	1,758	3,5	10	10	1 000

* First year mortality extrapolated from l_x data.

Table 43. Life table for female impala in Mkuzi Game Reserve in 1970–71, derived from mortality data and ages at death of 171 animals older than one year at time of death. See text for details.

Age x	f_x	Correction factor $e^{rx}(r=0,046)$	Corrected frequency $f_x e^{rx}$	$1\,000d_x$	$1\,000l_x$	$1\,000q_x$
0 – 1	75*	1,000	75	252	1 000	252
1 – 2	20	1,068	21,4	72	748	96
2 – 3	12	1,096	13,2	44	676	65
3 – 4	4	1,148	16,1	54	632	85
4 – 5	17	1,202	20,4	68	578	118
5 – 6	18	1,259	22,7	76	510	149
6 – 7	14	1,318	18,5	62	434	143
7 – 8	24	1,380	33,1	111	372	298
8 – 9	25	1,445	36,4	122	261	467
9 – 10	21	1,513	31,8	107	139	770
10 – 11	5	1,584	7,9	26	32	813
11 – 12	1	1,659	1,7	6	6	1 000

* First year mortality extrapolated from l_x data.

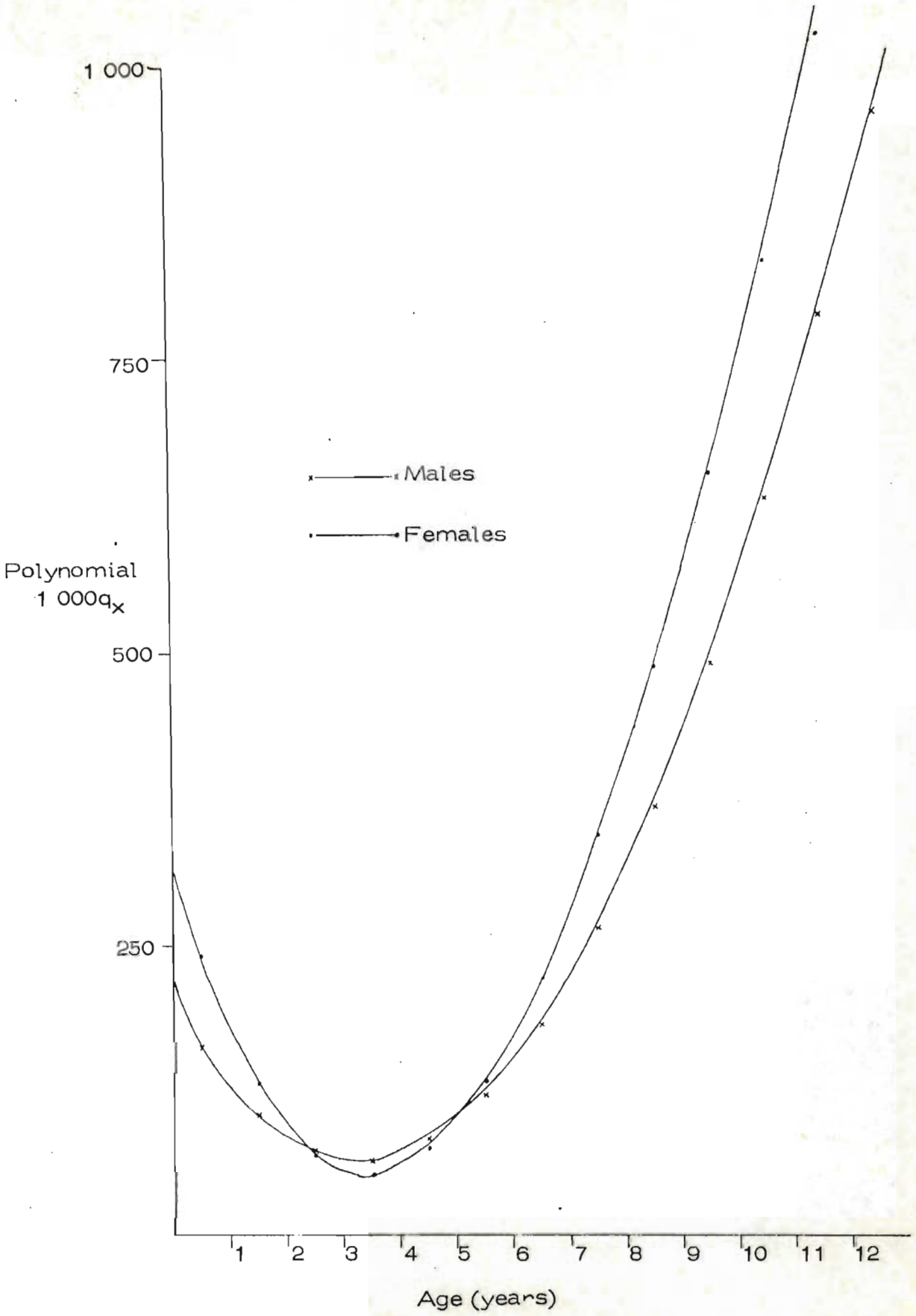

Figure 43. Polynomial plot of mortality rate (1 000q_x) data derived from d_x life tables.

carried out by the wildlife biologist.

The survival curve for males and females is plotted in Figure 44 and this too can be compared with that of Spinage (1972) and that derived from the l_x series in this study.

12.5. Discussion.

12.5.1. Life tables.

Caughley (1966) stressed the importance of the stable age distribution in constructing life tables from various sets of data, in particular from observations of the age structure based on age at death. However, Spinage (1970) made the point that such a situation is important only if a species as a whole is being considered. Thus, although a sample may be derived from a population that does not have a stable age distribution, a life table derived from the ages at death of a sample of the population may truly reflect the behaviour of that population, i.e. it is time-specific. Unless there is some powerful outside force influencing mortality beyond those normally doing so, the sample will present a true picture of age-specific mortality. However, it is seldom that two consecutive years impose the identical environmental influences on a population, so that no life table derived either in this way or from the standing age structure can be used to demonstrate the long-term demographic features. The best that can be shown are the features at that particular time, and that is what has been done here, without any effort to predict future population behaviour.

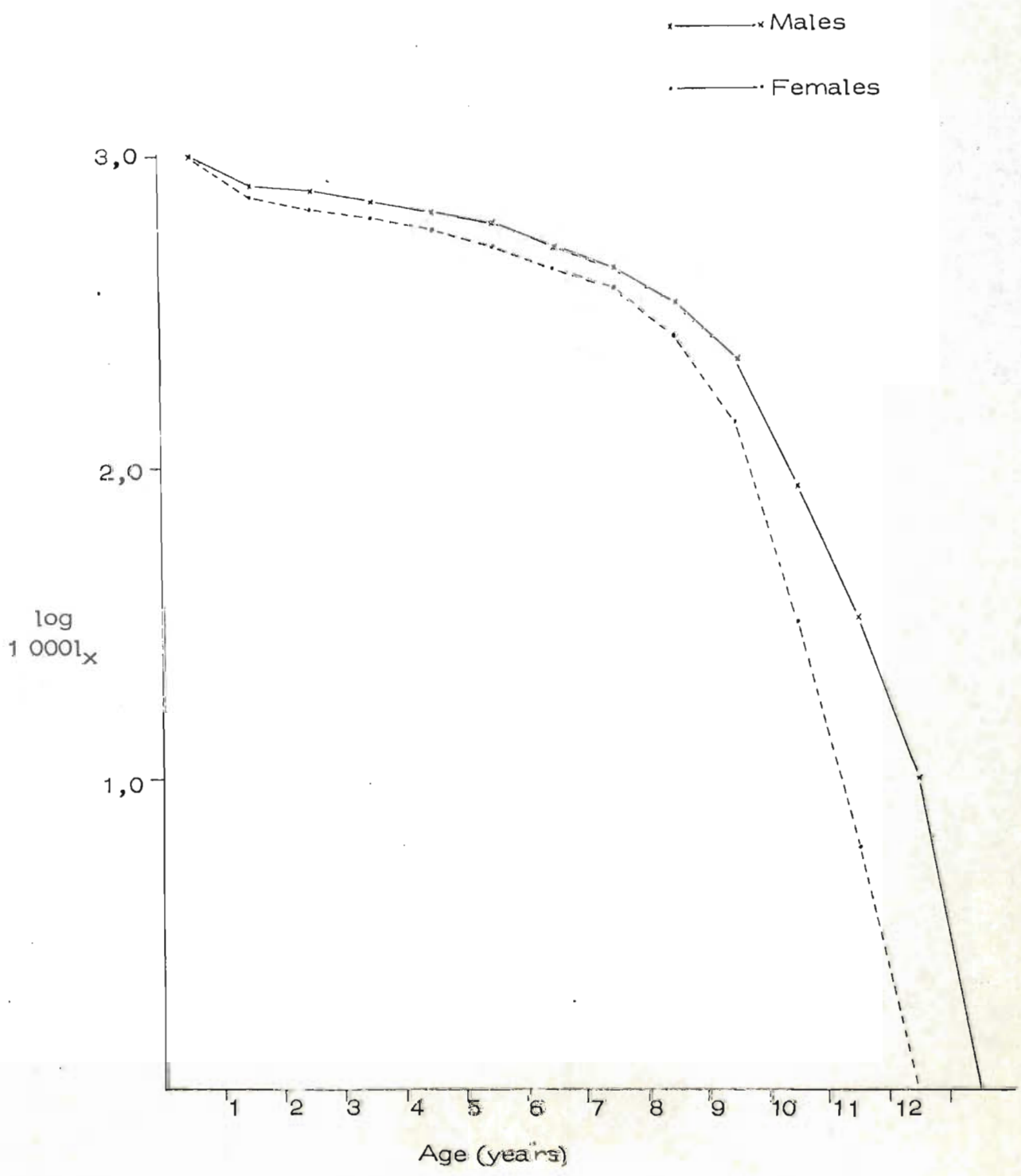

Figure 44. Log survival curve of impala in Mkuzi derived from d_x data.

The life tables also enable comparisons to be made between the demographic characteristics of males and females.

There are factors associated with the impala population of Mkuzi which make longer term analysis in terms of the life tables presented quite impossible. The most important of these is the population crash observed in the drought of 1966. There is no record of which age classes were most affected by this drought, but since it occurred only four years prior to the commencement of this study, its influence must still have been considerable. Although the population had recovered in numbers, the age structure observed must have been affected, and would be expected to have a bias towards younger age classes.

Marked differences are evident between the survival (l_x) and mortality rate (q_x) curves in both males and females when these are plotted from the l_x and d_x data. These differences indicate an apparently higher rate of mortality in the lower age classes, up to the age of about six years, when the data are derived from the l_x series than when derived from the d_x series.

In the case of the l_x series the standing population is being sampled, and the parameter q_x may thus be better described as the rate of loss than as the rate of mortality. The apparent absence of the younger age classes may therefore be due, not so much to mortality as to emigration from the study area. The d_x series, on the other hand, reflects the true rate of mortality and the fact that the younger age classes had left the study area means that there would have been relatively fewer present, so that there were of course fewer to die.

This theory accords with the findings of Hitchins and Vincent (1972) in which it was found that younger animals are those which leave the population to colonise new areas.

However the difference between the two rates of apparent mortality underlines a more fundamental difficulty which is that, contrary to what was expected, the study population is not a completely closed one, but it is subject to emigration. This fact must therefore be accepted in a study of the Mkuzi population and may be important in management considerations. It also accounts for the calculated rate of increase in Mkuzi being a great deal lower than would normally be expected in this species, with its high birth rate. Brooks (1978) estimated the rate of increase to be about 15% in the impala population in nearby Hluhluwe Game Reserve, while it was shown earlier in this chapter that the incremental rate for two year-olds was 25,7%.

Assuming a potential rate of increase of 25% and an actual rate of 5%, then about 12% of the population is lost to emigration and mortality. In a population of 18 000, this means that about 2 160 animals leave the reserve or die each year.

If emigration is a factor that must be considered then it also probably means that the Mkuzi population had, in 1970/71, reached the environmental carrying capacity of the reserve. Whether this acted socially or nutritionally is not clear, but the fact that vegetation assessment pointed to overutilisation suggests the latter. The average removal rate since 1971 has been about 3 000 animals annually, which would more than account for the annual increase less emigration assuming that this took place at the same rate. It also means that the population recovered

to the environmental capacity level in only four to five years after the drought of 1966. Possibly the effects of the drought on the impala population were not as drastic as had been thought.

It may also be speculated that the comparatively high mortality rate in the 7 to 10 year-old age classes seen in the d_x series points to a possible high survival rate of these individuals during the drought when they would have been 2 to 6 years old. It may well have been that they showed greater mobility at that time, moving away from the reserve to find water, and that they later returned to boost the population and help it to recover rapidly.

Successive seasons in the Mkuzi area may also differ considerably, so that the environmental influences on the impala population differ from year to year. For this reason time-specific life tables such as have been constructed are more valuable provided that they can be derived regularly if they are to be useful in management. In other words, regular monitoring of the population is essential for achieving management objectives.

A further factor which may influence the population structure is the removal programme and the method by which this is done, namely selection for females and younger males. The use of a helicopter in mass capture enables this selection to be made, and adult males to be excluded.

In addition to the difference in the forms of the mortality curves between the l_x and d_x series from which the conclusion that emigration takes place has been drawn, there is also a difference between the forms of the male and female mortality rate curves derived from the l_x series. There is a lower rate of "loss" of

females than of males up to the age of 7 years, although the reverse is the case for the first two years. This means that there is in fact a higher porportionate loss of females up to 2 years old, after which this changes. It suggests that the mechanism whereby the adult sex ratio favours females only comes into reckoning at this time, and not in the early stages as has been commonly thought to be the case.

The higher rate of loss of males is probably due to emigration, with the individuals not returning to the population. The fact that the rate of mortality of males derived from the d_x series is not higher than that of females (except between 2 and 5 years, and then only marginally higher) precludes deaths due to fighting as a significant mortality factor. This is despite the high recorded male mortality in May, June and July (see Figure 37).

The survival curves of impala in Mkuzi, when directly compared with those of Spinage (1972), who obtained his data from the ages at death of a sample, show the basic similarity of a convex curve. However, in the case of males particularly, Spinage found a concavity between the ages of 5 and 9 years. It is at this age that most animals were probably territorial and therefore most subject to predation which would tend to depress survival. Predation is not a major factor in adult mortality in Mkuzi, and this would account for the difference between Mkuzi and Rwanda impala survival.

The same configuration of a convex survival curve appears to be common to many ungulate species, e.g. red deer (Lowe 1969), waterbuck (Spinage 1970), and buffalo (Sinclair 1977).

12.5.2. Rate of increase.

The finite rate of increase e^{rt}, of Mkuzi impala between 1970 and 1971 was 1,035, and r is therefore 0,034. This appears to be rather low if the potential rate of increase of the species is considered. Brooks (1978) estimated the rate of increase to be 15% in Hluhluwe Game Reserve, and in Mkuzi the proportion of juveniles in the population in 1970 and 1971 was consistently more than 20%, whilst the incremental rate of two year-olds was 25.7%. This indicates that there is a potential for a higher rate of increase in the absence of factors such as predation and emigration.

However, as has been shown, there was a substantial rate of emigration from Mkuzi in 1970 and 1971, presumably on account of the high density which created excessive population pressure. The effects of this emigration, apparently of animals "in their prime" may be very important in the dynamics of the Mkuzi population. Robinette et al (1957) provided evidence that the sex ratio of mule deer Odocoileus hemionus varied significantly with the age of the dams: that there was a preponderance of males among first-born fawns. This accords with the findings in human demography (Scheinfeld 1943, Rosenhaupt 1939, quoted in Robinette et al 1957). Lowe (1969) found a complementary tendency in red deer Cervus elaphus, namely that animals "in their prime" gave birth to significantly more female fawns.

Whilst there was not enough evidence in the present study to substantiate these findings, such a situation would have a profound effect on population dynamics. It would serve as a

form of population control under certain circumstances. For instance, a population with a preponderance of young animals is generally considered to be growing, but if more males are being born into the population, this would have a depressive effect on the rate of increase as the sex ratio changed in favour of males. This may be in part the reason why a population, once it has declined to a certain level, can no longer sustain itself.

The finding that in impala there is an imbalance in the foetal sex ratio in favour of females was based largely on information from elsewhere. Because "prime age" animals in Mkuzi make up a comparatively small proportion of the standing population, the use of this data may in fact not be valid.

If the model described in Chapter 12.3 and Figure 42 is constructed using a sex ratio of unity and the same life table data, then the finite rate of increase, r, can be shown to be 1,018, and e^r is 0,018.

The conclusion to be drawn from the low rate of increase is that at the time of the study the population had practically stabilised, and the equilibrium level for Mkuzi is estimated at between 17 000 and 18 000 animals. This level is likely to fluctuate with changing conditions from year to year, and careful monitoring of the population is necessary for effective management.

CHAPTER 13

MANAGEMENT.

13.1. Introduction.

The dictionary definition of manage is, inter alia, "make proper use of". This in itself implies a human agency, and it is just this aspect which it is intended should be dealt with in this chapter.

Similarly ecology is the study of the interaction of all the factors influencing an area. The human influence is inextricably bound up in the ecology and management of Mkuzi Game Reserve, for it is this which has resulted in the need for a study of the sort reported on here.

Mkuzi Game Reserve is an area of little more than 23 000 ha surrounded on all sides by human settlement, which intimately affects the well-being and maintenance of the reserve. It is in fact an island which contains many elements that are seen as "natural" but which have all been affected in one way or another by its isolation, and therefore require some sort of manipulation. Management takes many forms, each requiring various techniques.

13.2. The aims of management for Mkuzi.

The management plan for Mkuzi Game Reserve states

that the primary aim of management is to "maintain the reserve as a living example of the fauna and flora which formed a natural ecosystem over a much wider area in this region before the advent of modern man". It goes on to say that this involves the maintenance of a diversity of species, the restoration of degraded habitat, and controlling the causes of this degradation.

Secondary objectives include the need to manage for human recreation, education, for research, and for the preservation of certain features.

The primary objective is strictly and logically unattainable if the secondary objectives are to be achieved, so that at best the management of the reserve can only ensure partial success in the restoration of the natural order. It is more important therefore to aim for the maintenance of an appropriate diversity of flora and fauna.

13.3. The management problems.

Before solutions and techniques can be applied, the problems requiring management must first be identified. Some of these are closely interrelated with one another, and the most important ones facing Mkuzi Game Reserve are as follows:

13.3.1. Water.

Little is known of the water regime of Mkuzi prior to the advent of modern man. However, anecdotal evidence

suggests that the Mkuze river was at least a more permanent river than it is today. Most of the bed where it forms the reserve boundary is sandy, with the exception only of a small section where it flows through the Lebombo mountains. Here it was once rocky, and within the last couple of decades has become severely silted up. The origin of this silt is mismanagement in the catchment area resulting in accelerated erosion. This in turn has resulted in greater surface runoff and less underground storage.

The situation today is that the river flows on the surface only after heavy rains in the catchment area. Surface flow ceases in nearly every dry season, yet twenty years ago this was a rare occurrence.

Apart from fairly scanty knowledge of the water regime of the river itself, nothing is known of the occurrence of surface water elsewhere in the reserve in earlier times. However, because of the nature of the soils and the comparatively low rainfall, it is unlikely that this would have been a feature. The only exceptions are the major pans such as Nhlonhlela and Nsumu which are filled by floodwaters from the river. These pans only drain when the river level drops substantially, and if it is accepted that the river level is no longer at it was, then it is likely that these pans were once less inclined to dry out than they are today.

Furthermore, similar pans on the Mocambique plain, which are associated with rivers less affected by catchment mismanagement, e.g. Pongola river, are

permanent in nature - or were prior to the construction of a major dam.

The supply of water to Mkuzi Game Reserve is therefore a vital management problem which requires continual attention during the dry season. In fact water has to be pumped from a well-point some distance beneath the river bed, to supply two waterholes artificially.

13.3.2. Soil.

Because of the extremely erodable nature of many of the lowland soils in Mkuzi, any disturbance either of the vegetative cover or of the soil itself results in erosion. Reduction in the vegetative cover has been one of the primary indicators of overpopulation of herbivores, and is a result of habitat overutilisation. Another major cause of soil disturbance has been the poorly planned construction, alignment and drainage of roads, of which there were many during the anti-nagana campaign.

To these factors must be added that of natural erosion. This has simply been speeded up by inadequate management, as a direct result of human interference with the ecosystem.

Remedial action on soil erosion is an ongoing management programme in Mkuzi. In established dongas it is necessary to use gabion structures combined with stone-packs; in smaller, more active dongas stone-packs alone are generally adequate; and where sheet erosion is a

problem, cut brush staked out in contour lines has proved successful. In some of the very active dongas the sides have been sloped using a bulldozer and the soil stabilised with anchored brush packs while seeding of grass is carried out.

13.3.3. Tourism.

One of the secondary objectives of management in Mkuzi is to provide for tourism. This may have an impact on the reserve in various ways. In the first place it is necessary to provide roads and these, if not properly designed, may cause erosion. Secondly the Natal Parks Board, in providing artificial water, has also constructed game viewing hides. Their location may not necessarily be in the habitat best adapted to withstand the inevitable high pressure from herbivores that develops in the vicinity of the only source of surface water in the dry season. Finally there is some disturbance from tourist activity, particularly on more "sensitive" species such as black rhino and cheetah.

13.3.4. Vegetative cover.

The combination of the poor soils, low rainfall and high herbivore population may result at least in local habitat degradation, particularly in those areas which are favoured habitat for those species with a high biomass, and in the vicinity of the permanent water. Degradation of the vegetation may take the form of changes in the species composition through overutilisation or of partial or

complete denudation.

Generally speaking the former results in either scrub encroachment, the development of annual grasses and herbs, or the development of an unpalatable grass cover. These features are all evident in various degrees in Mkuzi.

A further cause of veld deterioration is the injudicious use of fire. This may be the wrong time of the year, too frequent burning, or even insufficient burning. It has been accepted that fire is a factor in the maintenance of much of the woodlands or grasslands of Africa, and as a management tool it is invaluable if properly used.

13.3.5. Animal populations.

The aspect of management of most concern during this study is the control of animal populations, and in particular that of the impala.

There are unfortunately few records of the species present in the area before the advent of modern man, and it has been largely a matter of guesswork as to whether a particular species is being introduced or reintroduced. Certain species have always occurred there, but others have been put there within the past 20 years. Of these, the white rhino and cheetah have fared very badly, whilst the giraffe has shown a phenomenal rate of increase, from seven released in 1965 to more than 60 today, a mere 14 years later. There is some doubt as to whether giraffe occurred in the area before this time. Species known to

have occurred but absent today are elephant and lion, while the former presence of buffalo is only a possibility.

Thus our knowledge of the components of the ecosystem is largely inadequate, yet it is necessary to rely on this to restore the "natural ecosystem" as required by the management plan. An example of the way in which the present habitat may be changed lies in the fact that a favourite food plant of giraffe is Acacia nigrescens, yet the ability of this plant to regenerate sufficiently fast to support a larger population than at present is in question.

This in fact is the basis of the whole problem of animal population management - the manipulation of numbers to ensure optimum or sub-optimum use of the habitat. To achieve this it is not sufficient to know only the dynamics of the various animal populations, but necessary to understand also the dynamics of the vegetation and the interrelationships of plants and animals.

A further factor which has influenced the management strategy for Mkuzi is it increasing isolation. Human activity on all sides of the reserve has made it difficult for animals to disperse or to migrate, resulting in utilisation of available resources by essentially the same numbers of animals throughout the year, and preventing them from obtaining a rest as probably occurred in former times.

Yet another factor is the comparative paucity of natural predators which has meant that the rate of

increase of most species has been unaffected by predation. Thus the reserve manager had had to adopt the role of "stand-in predator", achieving his end by culling or capture.

Whilst these comments are true of several species of ungulate, they apply most particularly to the impala which, as has been shown, makes up more than half the total biomass of the reserve.

13.4. Impala management.

On the effective management of the impala population in Mkuzi depends the survival of the game reserve. In the absence of predation and the inability to disperse, and in consideration of all the aspects of management described above, the need for population control is incontrovertible. It is only the level of control which remains to be rationally determined, and the aim of this paper was to provide some of the answers which would help in this decision.

Before making some recommendations as to the future management strategy, a brief summary follows of some of the more important points arising from this study:

1. Census. The use of aircraft as a means of estimating numbers of impala in Mkuzi is ruled out as being of any value. The alternative of road strip censussing using a fixed visibility profile seems to be reasonably accurate and

probably gives an accuracy to within at most 10% of the true figure.

2. Ageing. The establishment of an age structure is fundamental to an understanding of the dynamics of a population and hence to devising its management. The method of ageing using molar height seems to provide a reasonable method of age determination.

3. Behaviour. The existence of a seasonal cycle of behaviour, related to seasonal breeding, is an important factor to consider in management.

4. Reproduction. The fact that reproduction is strictly seasonal will influence the management of the Mkuzi impala population.

5. Distribution. An understanding of the seasonal distribution patterns, probably related to vegetation phenology, provides information of use to the manager.

13.4.1. The aims of management.

The main objective of the management of the impala population should be to maintain a balance between the habitat and the animals so that degradation of the former does not occur, for this in turn will reduce the productivity of the primary resource, and therefore of the herbivores, and ultimately affect the tourist potential and aesthetic attraction of the reserve. Furthermore, it is important to maintain the impala population at such a level that other herbivores

are not affected, thereby retaining the desired diversity.

Any situation in which the manager aims to achieve maximum productivity of impala, because he is influenced by a need to achieve a sustained yield for economic reasons, must be avoided. This would be a case of the "tail wagging the dog", for the objectives are species diversity and habitat conservation - not maximum sustained yield. This is the aim of the game rancher for whom there is a different place in the overall scheme of conservation.

Further, the need to conserve the species per se is no longer necessary.

13.4.2. The management strategy.

As a basis for management this study forms only a part, for the vegetation dynamics of the reserve plays an equal role. A first priority is therefore a detailed vegetation study of Mkuzi Game Reserve to determine the status of the important impala habitat.

A second priority is studies of the important herbivore competitors of impala in the reserve. Nyala are probably the main competitor, followed in importance at present by warthog and wildebeest. Their relationships with the habitat and with impala are essential elements of knowledge for a full assessment of a management strategy.

In so far as impala management is concerned the following procedures are considered necessary in the future:

a) Regular monitoring of the number of animals present. Intensive road strip censussing three or four times a year would achieve this end.

b) Regular monitoring of the age structure of the population, although it is doubtful whether any more detailed knowledge than simply of the numbers of juveniles, immatures, young adults, and old adults is necessary.

c) As a means of reducing competition for available browse, and because this is important in winter particularly and it has been reduced by range restriction, the numbers of nyala need reduction. The level to which this is necessary can only be determined after a study of this species.

d) As a means of reducing competition for grass, the numbers of warthog must be prevented from increasing beyond a limit to be determined. These are, in part at least, self-regulatory, for warthog are severely affected by dry seasons. However the species does have a very high capacity for recovery in favourable seasons.

e) Because of habitat degradation that was evident in the presence of about 17 000 animals during this study, a reduction in the number of impala to a level of about 12-13 000 seems desirable. It must be remembered though that the period of the study largely coincided with the end of a dry cycle of years, so that more favourable seasons, with higher rainfall, as occurred in the

subsequent six to seven years, should enable a higher population to be supported. However, management should always take into consideration the stresses imposed on the habitat by a dry season.

f) Having reduced the impala population to what is considered to be the optimum level of 12-13 000, the annual removal rate can be set at about 15 - 20%, i.e. about 2 300 per annum. This removal should be unbiased towards any one age or sex, and the procedure should aim to remove the animals in approximately the proportions of the standing population.

The present techniques of removal, whereby females and juveniles are selected by live capture and males are selectively shot, would appear to be satisfactory. However, there is a tendency towards leaving young males, and an improvement may be effected by reducing the number of adult males shot and increasing the number of immatures. At a removal rate of 2 340 per annum, about 470 adult males and 200 immatures would achieve the necessary proportions.

APPENDIX

The following description is that of the generalized procedure for the plotting of points on probability paper, to determine the approximate fit of linear transformations in a series of overlapping frequency distributions.

Step 1. Plot the cumulative precentage distribution of the relevant parameter, e.g. molar height, of the suspected multimodal sample.

Step 2. Determine the points of inflection of the plotted fit, recognizable by eye as having a steeper slope. Let these points be $p_1, p_2 \ldots\ldots p_n$ on the horizontal scale.

Step 3. Extract the first distribution (d_1), i.e. up to the first point of inflection, by multiplying the original percentage frequencies ($f_1, f_2 \ldots\ldots f_n$) by $100/p$.

Step 4. Plot again, on the same paper, the points of this distribution, and fit a straight line to this by eye.

The n^{th} distribution is extracted as follows:

$$d_n = (f_{n_{1,2}\ldots\ldots n} - p_{n-1}) \times 100/p_n - p_{n-1}$$

The degree of overlap between successive distributions is recognizable by, and proportional to, the number of points lying to the right of and below the fitted line, and the extent to which they do so. In the event of such overlap occurring,

it is necessary to make corrections in the succeeding distribution.

The first point on this new distribution is determined from that percentage frequency immediately below the point of inflection (p_{n-x}). Let the percentage on the n^{th} distribution represented by this level of the parameter, be a_n; then the percentage of the total sample represented by the n component will be:

$$a_n(p_n - p_{n-1})/100.$$

To this must be added the percentage represented by the n-1 component, so that the total percentage of the sample represented to this point is

$$a_n(p_n - p_{n-1})/100 + p_{n-1}.$$

Then the first point on the new curve will be

$$(p_{n-x} - (a_n\ p_n - p_{n-1}\ /100 + p_{n-1})) \times 100/p_{n+1} - p_n\%.$$

As soon as a point on the new distribution corresponds to nearly 100%, the correction need no longer be applied, and the point on the new distribution is obtained by:

$$((p_n - p_N) - p_n)100/p_{n+1} - p_n,$$

where p_N is the percentage frequency of the point corresponding to nearly 100% on the old distribution.

The analysis of the data is worked as follows:

Distribution	$\bar{x}$	s	% of total	Number in distribution.
1				
2				
3				

where $\bar{x}$ = mean of measurements, determined by the point at which the 50% cumulative frequency intersects the fitted linear distribution;

s = standard deviation, calculated by the difference between the measurement of the parameter at 99,9% frequency (edge of paper) and at 50% (mean), multiplied by 3,72;

% of total = f_n;

No. in distribution = $f_n \times$ sample size/100.

SUMMARY

The need to understand the dynamics of the impala population in Mkuzi Game Reserve arose during the early 1960's when it became clear that various factors were contributing to an overpopulation of the species in the reserve. Population management was recognized as being necessary and was carried out, but it was based on inadequate information.

This study set out to establish a rational basis for future management. The social organization and behaviour of impala in Mkuzi were analysed and placed in perspective relative to the population dynamics. Two methods of counting the animals were used and a relationship obtained between the respective results. The distribution of impala within the reserve, both on a gross population basis and with respect to the various sex and age categories, was determined from sampling. In order to establish the age structure of the population, samples obtained from the control programme were used, and these were aged on the basis of molar wear. At the same time the proportions of young animals and the population sex ratios were obtained by field sampling.

Using these data, life tables were constructed, from which it was possible to interpret the behaviour of the population at the time of the study. However, caution should be exercised in extrapolating these results literally to the same population under different conditions. The study only provides guidelines for regular monitoring to be carried out. At the same time a more detailed study of the vegetation dynamics of Mkuzi Game Reserve is a priority so that the relationship between the animal and plant elements of the reserve can be properly analysed.

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